PLANT ECOLOGY
GENETICS AND EVOLUTION

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(FOR B.Sc. & AGRICULTURE CLASSES)

BY

P. L. KOCHHAR, *M.Sc.* (*Hons.*)

Author of :
"A Textbook of Plant Physiology" and "Pre-University Botany"
and Co-author of "Intermediate Botany", "Foundations of Biology"
"Pre-Medical Botany" and "Madhyamik Vanaspati Shastra"

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PREFACE

SEVENTH EDITION

In this, the seventh edition the general plan of the book has been retained but within this framework the text has been thoroughly revised and some important changes and additions have been made throughout the text. The articles on mitosis, meiosis, cytoplasmic heredity and chromosomal mutations have been rewritten and chapters on the "Nature of the genetic material" and "plant breeding" have been improved and enlarged. A few new illustrations have been added and some of the old ones have been improved.

Comprehensive, up-to-date and abundantly illustrated with line drawings and photo plates, the book contains a wealth of information useful to the student.

In the preparation of this and the earlier editions of the book I have received valuable suggestions and generous help from several teachers in the country. In this connection I am especially indebted to Professor U. K. Sinha, Town Degree College, Ballia; Professor M. C. Saxena, College of Science, Raipur; Prof. R. Beliram, Hislop College, Mahal, Nagpur; Prof. M.S.S. Rao, Basaveshwar College, Bagalkot; Prof. K.C. Sheriar, Jai Hind College, Bombay; Dr. B.S. Navalkar, the Institute of Science, Bombay; Dr. V.R. Dnyansagar, Head of the Botany Department, Institute of Science, Bombay; Prof. H.D. Noronha, Gujarat College, Ahmedabad; Prof. A. B. Saran, Head of the Botany Department (Retired), Bihar Agricultural College, Sabour, Dr. A.K. Gupta, Associate Professor of Genetics, Punjab Agricultural University, Ludhiana and Professor G. D. Patil, College of Agriculture, Kolhapur.

I am especially indebted to Dr. V. P. Gupta, Geneticist, Punjab Agricultural University, Ludhiana for guidance and for contributing an article on the breeding of fodder crops.

Further criticism of the book and suggestions for its improvement will be welcomed and are hereby solicited.

29, Nicholson Square P. L. Kochhar
New Delhi-1
June 30, 1972

FIRST EDITION

Although one of the youngest branches of biological sciences, genetics has made great and rapid progress within the last two or three decades. The knowledge of thirty years back has almost gone out of date. The reason for this lies in the great importance of the subject in plant and animal breeding and also on account of its significant bearing on the problem of evolution. While there are quite a number of excellent books devoted entirely to genetics or evolution, or both, the books on general botany which are offered as textbooks for students preparing for a degree in botany contain only a very brief account of these subjects. It is my opinion that students should know more about these subjects. Rather, every educated person should have some knowledge of them. Hence this book, which is intended primarily for B.Sc. pass course students in botany. The subject has been dealt with in slightly greater detail and it is hoped that the book will also be useful to students preparing for an honours degree in botany or zoology.

Originally, it was intended to confine the book to genetics and evolution but later on the scope of the book was enlarged to include plant ecology also. This was done on the recommendation of the publishers who had received several requests in this context from teachers and students.

In writing this book, I have freely drawn upon a number of English and American books, and to their authors and publishers I wish to acknowledge my indebtedness.

I am also greatly indebted to Prof. P. C. Joshi, Ph.D. for lending some very useful photographs and to Prof. B. N. Sood for taking some photographs for this book.

It is hoped that the book will be found useful in spite of its shortcomings and deficiencies. Suggestions for its improvement are solicited and will be welcomed.

Nov., 1959. P. L. Kochhar

Printing Errors

Part 2

Page	*Line*	*For*	*Read*
207	40	Maxico	Mexico
		TN-variety	TN-1 variety
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229	15	mutattion	mutation
236	4	natural	neutral

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PART I
PLANT ECOLOGY

THE ENVIRONMENT

THE SCOPE OF PLANT ECOLOGY

PLANTS are found all over the earth, growing in all kinds of situations. They are found growing on the tops of high mountains which are covered with snow for the greater part of the year and in the hot springs ; they grow on the moist banks of streams and in the dry sand of deserts or even on dry rocks ; they are found also growing in the crevices of walls and some lie perched on the trunks of trees. In fact, there is hardly a place on this earth where plant life of one type or another is not met with But the species that inhabit this earth vary from place to place. It is common knowledge that the water-lilies and the pond weeds that grow in water are wholly absent from the neighbouring dry land. In like manner, the oaks and the walnuts which we come across in the mountains are not represented among the plants that grow in the plains. Again, the luxuriant vegetation of places situated at the foot of a mountain, like Dehradun, where plants of many species grow, contrasts greatly with the sandy desert of Rajasthan where not only the plant cover of the soil is scanty but the species are also few and different.

The distribution of plants on this earth is not haphazard. The [illegible]

of the environment is habitat by which is meant the particular place or situation in which a plant grows, e g the bank of a stream or a sandy slope, a marsh or a tree trunk. Habitat is more specific in meaning than environment as a whole. The branch of botany which

deals with the specific study of relationship of plants in relation to their environment is called **plant ecology.** The term 'ecology' is made up of two Greek words, *oikos*, meaning home, and 'logia', meaning study. In brief, plant ecology describes the home life of plants. It brings out the physiological relationships between the plants and their environmental conditions. It aims at explaining why certain plants grow and are associated together in particular habitats and why they do not grow in others.

The reason why species are not uniformly distributed over the earth's surface is that environments differ from place to place and so do the plants Plants growing in any particular habitat are fully adapted to live in that habitat. In other words, they are in complete harmony with the factors of the environment. This adaptation of a species is called its **epharmony** A species that cannot adapt itself to the natural conditions under which it lives must perish and dis appear from that environment. The same thing happens when the environment undergoes a change to which a species cannot adapt itself. It is thus the environment that determines the destiny of a species ; it determines whether it shall survive or perish.

Epharmony may be achieved in a number of different ways Thus, one species may adapt itself to the dry habitat by means of a dense coating of hairs ; another may not have a single hair but may develop a waxy cover on the leaves or else reduce its foliage ; still another may assume a succulent form or else become ephemeral in its life-history. On the other hand, species belonging to widely apart families may be extraordinarily alike *in their habit, form* and structure. A striking example is afforded by the cacti and the cactus-like species of *Euphorbia*. It is one of the objects of plant [illegible] tructural and physiological pecu- [illegible] ljust themselves to different envi- [illegible] morphological and a physiological study.

There are two aspects of plant ecology, **autecology and synecology.** The former is concerned with the study of individual plants or factors; synecology is the study of plant communities or complexes of factors Closely allied to plant ecology **is plant geography** which deals with the distribution of plants over the earth and attempts to account for the distribution and migration of species

FACTORS OF THE HABITAT

All organisms, including plants, must live in some sort of envi-

ronment. Their physiological processes, which are essential for the maintenance of life, are dependent upon environmental conditions and substances. Many of these processes require water; food manufacture by plants is dependent upon carbon dioxide and light; respiration requires oxygen; and all processes are influenced by

in the ecological factors. Regions which have a similar set of ecological factors will have similar vegetation because the demands of the environment on the plant under similar conditions are similar. All the environmental factors do not influence the plant equally. Some, e.g. the amount of oxygen and carbon dioxide in the air, differ so little in different places that they have no ecological significance. Others, *e.g.* the chemical and physical nature of the soil, the relationships between plants and animals, and between plants themselves, vary so widely even in smaller regions that they cannot be used for limiting ecological regions; but, on the other hand, they are useful in the detailed analysis of vegetation within these regions.

All the environmental factors can be arranged in four groups, namely (1) **climatic**, which relate to the aerial environment of the plant; (2) **topographic**, which relate to the form and behaviour of the earth's surface; (3) **edaphic** or soil factors like physical and chemical nature of the soil which operate within smaller and localised limits; and (4) **biotic** factors or the effects due to the activities of other plants, and animals including man. The various factors under each of these groups are tabulated below:

1. *Climatic factors*	2 *Topographic factors*	3 *Edaphic factors*
Precipitation	Altitude	Mineral component
Atmospheric humidity	Surface	Organic component
Wind	Slope	Soil water and solutes
Temperature	Exposure	Soil air
Light		Soil organisms
		Soil reaction

4. *Biotic factors*

Though the various factors are dealt with in this book separately it must be borne in mind that they never work singly but work in

nodifying the effects of one

decide what may be attri-

Some factors affect plant

life directly while others affect indirectly by modifying other factor as given below :

Direct factors	*Indirect factors*
Humidity	Precipitation
Light	Soil structure
Temperature	Wind
Soil water	Altitude
Soil solutes	Slope
Soil air	Soil flora and fauna

Of the direct factors listed above, the water content of the soil determines absorption of water by plants; humidity and temperature determine transpiration and light affects photosynthesis. Soil solutes are responsible for plant nutrition and soil air is necessary for the respiration and normal functioning of roots. Precipitation and soil structure have an indirect effect on absorption through their effect on the water content of the soil. Precipitation also modifies the vapour content of the atmosphere and thus affects transpiration. Wind affects plant life in a like manner. Altitude affects humidity by its effect on temperature and precipitation. The soil flora and fauna also influence plant life in an indiret way but one which is of great significance to plant life. Thus, the saprophytic fungi and bacteria bring about the decay of organic matter coming from the dead remains of plants and animals and convert it into simpler compounds and in this process release soluble minerals which are so valuable for plant nutrition. The nitrogen-fixing and nitrifying bacteria increase soil fertility while the denitrifying bacteria have an opposite effect. The earthworms increase soil aeration and bring about a mixing of the soil.

CLIMATIC FACTORS

The chief factors of the climate are precipitation, humidity, temperature, light and wind. While these factors are subject to more rapid fluctuations than the edaphic factors, they are usually almost constant over large regions. Consequently, these are the ones that more than all the others determine the types of vegetation over large areas, for all plant communities are subject to their influence. Differ- [illegible] factors account for different types of [illegible] different types of vegetations all over [illegible] of Rajasthan and Sind produces a desert, that of the Punjab and North Gujarat a semi-desert and that of Central India and Eastern and Western Himalayas different types of forests

1. Precipitation. The principal forms of precipitation are rainfall, hail, snow and dew. Of these, rainfall is the most important as most plants absorb water from the soil. Lichens, some epiphytic orchids and a few other plants can absorb moisture directly from the atmosphere. As already stated, precipitation is an indirect factor which affects plant life through atmospheric humidity and water content of the soil. It may, however, be stated that the vegetation of any great region is determined primarily by the amount and seasonal

water absorption from the cold soils is precarious. In regions with heavy rainfall in winter and low rainfall in summer, which is hot, the forest is of a sclerophyllous type, that is, it is composed of low trees or shrubs with broad leathery, evergreen leaves which can function during winter and are able to withstand the summer drought.

Lighter rainfalls correspond with climate grasslands. Grasslands require growing-season rainfall. They are, therefore, found in regions characterised by heavy summer rainfall, and low winter rainfall. Regions with very low rainfall both in winter and summer correspond with deserts.

The above facts about the influence of precipitation on the distribution of vegetation types are expressed in Schimper's Third Law which states that in tropical and temperate regions, the type of

sonal distribu-

a more signi-
ture because it
It influences the rate of trans-
of water vapour in the air or
conditions the rate of water

precipitated in the form of rain, dew or snow. In such an atmosphere

air such as that of a desert may actually contain more water vapour than a moist air and yet be able to take up more moisture because of its high temperature. With the absolute humidity of the air remaining constant, its saturation deficit increases with rise in temperature, and falls with the lowering of
falls very low, some of the mo
liquid water as happens in dew
to $R—P$ where R is the total amount of water vapour required to completely saturate the air at a particular temperature and P is the amount of vapour actually present, *i e.* its absolute humidity. Vapour pressure is a measure of the quantity of water vapour present in the atmosphere, the temperature being constant. Therefore, **vapour pressure deficit** is the difference between the amount of water vapour actually present and the amount that could be held without condensation at the same temperature.

The absolute humidity is often expressed as a percentage of the amount necessary for saturation at a particular temperature. This is called **relative humidity** and is equal to $P/R \times 100$. For example, 40 per cent relative humidity means that the air contains two-fifth of the total amount of water vapour necessary to saturate it. In other words, the air can still take up 60 per cent more water. The relative humidity decreases (or increases) with every rise (or fall) in the temperature while the absolute humidity remains unaffected. The lower the relative humidity of the air, the higher is the rate of eva-
y thus depends both
present. As a consequence, identical relative humidities do not indicate identical moisture conditions unless temperatures are also the same.

An atmosphere 70 per cent saturated at 30°C will be relatively wetter than an atmosphere 70 per cent saturated at 40°C and the capacity to hold more water will be less in the first case than in the second case Evaporation and transpiration will, therefore, normally be more rapid at 40°C even if the relative humidities are the same. Relative humidity alone, therefore, gives little indication of atmospheric moisture conditions since a relative humidity of 80 per cent may mean "dryness" if the temperature is high or "wetness" if the temperature is low.

Vapour pressure deficit, or the amount of water that air can take up before it becomes saturated, is a direct indication of the atmospheric moisture conditions, quite independently of temperature, and, therefore, compared to relative humidity its values are much more indicative of the potential rate of evaporation.

Precipitation and evaporation from the soil and transpiration from the plants *bring about an increase in the humidity of the air.* For this reason the air beneath an oak forest, for example, is more humid than that in the open. Humidity by its direct influence upon transpiration must determine what kinds of plants can grow in any given situation. Thus, in the humid air of an oak forest only delicate and moisture-loving species abound.

3. Wind. Wind has both a direct and an indirect effect on plant life. The direct effect of strong winds is mechanical and consists in uprooting trees and breaking off branches and twigs. Strong winds [illegible] osed places where [illegible] with few branches and leaves on the windward side. Grasses and other low plants or those with well developed rhizomes are less susceptible to winds.

The indirect effect of wind is physiological. Transpiration makes the air surrounding the plants moist. Winds remove this moist air and bring in dry air and thus increase transpiration. Consequently, the rate of transpiration is higher in places where winds blow than in still air. Winds blowing from the sea and other large reservoirs of water bring in moist air and hinder transpiration. Wind velocity increases with height above the ground. The plants with prostrate habit with their leaves near the soil surface are comparatively safe from the drying effect of wind while the tall trees are the greatest sufferers from excessive transpiration. Strong winds in the upper strata of the air cause the upper shoots to dry off and inhibit growth in length. In exposed situations, therefore, the wind action often limits the height to which trees can grow. In such places the taller trees grow to a uniform height called the "general vegetation limit". The same is true of trees growing on the windward side of a grove. These trees are usually less tall than those in the rest of the grove. *On exposed mountain ridges and flat sea-coasts tall plants are entirely absent.*

The exposed alpine r [illegible] by very strong winds. [illegible] and herbs become dwar [illegible] rhododendrons and silver fir, which a few hundred feet below are upright tall trees, remain short and shrubby and form what are known as elfin scrubs.

4. Temperature. Temperature regulates all the chemical [illegible] e [illegible] h [illegible] e

called the **optimum**. Further rise in temperature is accompanied by a fall in the metabolic activity until it ceases at a temperature called the **maximum**. Each species has its own minimum and maximum beyond which its life activity ceases. The plants are like the cold-blooded animals in as much as they have no fixed internal temperature. This varies with their environmental temperature. As we move away from the equator the external temperature gradually falls. The temperate zones are characterised by cold winters and in the arctic regions very low temperatures prevail. Although plants in general can live in a wide range of temperature conditions, they become accustomed to the temperature conditions of their habitat by constant association with the result that the habitat of a species comes to be more or less restricted to a definite temperature range. This may vary greatly for different species and depending upon the amount of water in the protoplasm may vary for individuals of a species. Some of the algae in the arctic regions remain active at temperatures far below 0°C, in sub-arctic alpine forests temperatures as low as—27°C have been recorded; and many species in the alpine regions remain buried under the snow without dying. The alpine [illegible] climate lower down. The [illegible] he alpine regions. Similarly, [illegible] temperate regions have to endure low winter temperatures. It appears that these low temperatures are necessary for stimulating the growth of such plants.

Plants of many species are killed by winter frost. The death in such cases is not due directly to low temperature but to desiccation, which occurs when water on the cell walls freezes in the intercellular spaces and consequently water is withdrawn from the vacuoles and protoplasm. In some cases, death may be caused by the rupturing of the cells due to the mechanical pressure of the ice because expansion takes place when water freezes. Injurious chemical changes, such as precipitation of cell proteins, may accompany the desiccation.

Many plants are resistant to low temperatures. Rather, periodical low temperatures (below zero) are necessary for them. Their seeds will not germinate and tubers, bulbs etc., will not grow until they have been subjected to freezing temperature. In others, resistance to low temperature can be induced by hardening, *i.e.* subjecting the plants to near freezing temperatures for a few days. Seedlings of garden and vegetable plants are treated in this way before being transplanted to the field. The same object can be achieved by subjecting the plants to drought. Tree seedlings are hardened in this way in nurseries before transplanting. Plants subject to winter-killing

show several modifications of metabolism which result in increased hardiness. The reserve starch is often converted into fats and oils or sugars. Sugars lower very much the freezing point of water and increase osmotic pressure. Proteins are often converted into soluble forms that are less easily precipitated. Hydrophilous colloids with high water-holding power like pentosans, mucilages and pectic substances are produced in abundance and further decrease the danger from desiccation.

The maximum temperatures that the plants can endure also vary with different species. While most plants live where the maximum temperature seldom exceeds 40°C, there are species of plants which can endure the much higher temperature of hot deserts which sometimes reaches 70°C. Most other plants will quickly die under such conditions. Very dry seeds and spores in dormant condition are practically without water and can withstand very high temperatures (even 100°C) which will kill the same species in an active state.

The optimum temperature at which a plant thrives best also varies with different species. It also varies for the same species with the season and the stage of its development. It is because the plants vary so greatly in their ability to stand extremes of temperature that they are found to grow successfully under many and diverse conditions of temperature.

As stated above, different species of plants vary greatly in the temperatures that they can endure. We might as well say that different species have different temperature requirements. Tempe-

[illegible]

different in different zones The same is true of grasslands and deserts. This points to the conclusion that while the general type of vegetation (*i.e.*, forest, grassland or desert) is not related to temprature, the flora of a region (*i.e.*, the individual species that occur

[illegible]

forest (*Shorea robusta*) ; *pinus longifolia* begins at about 3,000 ft., *P. excelsa* at about 6,000 ft., *Picea morinda* at about 7,000 ft., and *Abies pindrow* at about 7,500 ft. Of the broad-leaved plants, three species of oak occur ; *Quercus incana* begins at about 4,000 ft., *Q. dilatata*

at about 7,000 ft. and *Q. semicarpifolia* at 8,000 ft. The altitude at which a particular species occurs is higher on the southern slopes (being warmer) than on the northern slopes (being cooler).

Schimper's law of heat requirements applies also to crop plants. Each crop plant requires a certain number of effective heat units before it can mature. This is called the **thermal constant** and varies with the crop plant. Several attempts have been made to work out the thermal constants of crop plants.
minimum are effective in furthering a
these alone are *considered in working*
crop plant. The effective minimum temperature or plant zero, as it is sometimes called, varies with the crop plant and is fairly uniform wherever the crop is grown, being influenced but little by other conditions of the environment. For each crop plant the mean temperature of the average date of planting is regarded as the plant zero for the crop. It is 37°F for spring wheat, 43°F for the spring oat, 45°F for early potato, 55°F for corn (maize) and 62°F for cotton. Farmers all over the world have by long years of experience unconsciously learnt the approximate time when a particular crop must be sown. This corresponds to the minimum effective temperature.

One of the methods for working out the thermal constant of a crop plant is the method of summation. All mean daily temperatures above the effective minimum during the growing *season are added* together. Thus, if 43°F is the minimum effective temperature, then a day with a mean temperature of 53°F would count as 10 units, the one with a mean temperature of 58°F as 15 units, and so on. The thermal constant for corn from planting to harvest as worked out in America is 1,600 to 1,800 units depending upon the variety of corn grown, and 1,900 for cotton. A knowledge of the heat requirements of various crop plants expressed in terms of temperature and time would be of great advantage to agriculture. From the above data it would appear that cotton requires a warm climate and would grow better in the southern parts of India than in the north and that it would require more days than corn during which the temperature rises above the minimum. If a cotton variety were developed with lesser heat requirement, the area of its cultivation could be extended northwards.

5. Light. Ligh
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growth and othei
chlorophyll form
Chlorophyll prod

intensity and most plants are able to produce chlorophyll at light intensities considerably below those necessary for effective photosynthesis. In the cc

also develops in the

necessary for the fur

is also an important factor in transpiration which keeps down the

season, latitude, altitude and conditions of the atmosphere. On all places at the equator, light falls for twelve hours a day throughout the year. The days become progressively longer during summer as you move away from the equator. Light intensity also increases with altitude. Humidity tends to reduce light intensity. It is greatly reduced by heavy clouds and fog. A layer of water greatly reduces light intensity. Submerged plants, therefore, receive very weak light and at about 15 ft. depth photosynthesis is almost insignificant. The

are best suited to absorb and utilise. Green algae live along the

hat deeper and red algae

permatophyta are confined

to grow at greater depth.

The light that reaches the floor of a forest is also very weak on account of the shade cast by the foliage of the trees. Slopes also affect light intensity. It is greater on south-facing slopes than on a level area and least on a north-facing slope.

Plants may be exposed to strong light as in open places and alpine

to the mid-day sun.

s a por-

in shade

ige. In

many plants, the leaves are fitted together like stones in a mosaic. This mosaic arrangement reduces overlapping to a minimum and

ensures that every leaf will receive light. Many plants have a rosette habit in which the leaves are arranged in a circle on the ground as in dandelion. The rosette arrangement reduces overlapping to a minimum. Where overlapping occurs, the lower leaves are larger and light falls on some part of them. Some plants display their leaves to sunlight by growing as epiphytes high on the trees. In the grasses and allied plants (sedges, rushes and cattails), the leaf arrangement reduces the shade cast by the upper leaves so that almost all the leaves, even those at the base, are illuminated.

In the coniferous trees, the tapering trunk bears branches which become progressively shorter towards the apex. The leaves are developed mostly near the tips of branches. The arrangement is ideal for maximum illumination. Where the trees grow in close formation so that they cast a deep shade, the lower branches usually soon die and drop off because of poor light. The almost hemisperical crown of the deliquiscent trunk of the banyan or mango tree is similarly advantageous for the purpose.

The stem twiners and those that climb by means of tendrils, hooks, spines or roots have solved the problem of exposing their photosynthetic organs in a very economic way without much expenditure of material to hold their stems erect. A grapevine, for example, with a thin stem may have a foliage area as large as that of the tree which supports it, although the latter has a trunk several times thicker. From the fact that such plants are abundant in the forests and almost lacking in the open vegetation, one might conlcude that this habit must have resulted from the struggle for light.

Light inhibits the production of auxins or growth hormones. As

[illegible]

under a forest canopy, tend to be tall with long internodes and relatively few leaves. The better the light, the stouter and more compact the individual will be. This effect of strong light is evident in the alpine herbs which grow on exposed mountain tops.

[illegible]

the other.

The above mentioned effect of light on plant growth is responsible for the phototropic responses of aerial parts of plants. Incidentally, it enables the green plants to avoid strong light which has the effect of destroying chlorophyll and also inhibits its production.

Ligh [illegible]
way. T [illegible]
growing [illegible]
shade-le [illegible]
appears to be related to the light factor. Strong light increases palisade development in leaves. In sun-exposed leaves it often consists of two or more layers, and the cells are compact. Sometimes, the mesophyll of leaves growing in fully exposed places is all palisade, while plants of the same species growing in deep shade may have leaves with scarcely any palisade. This explains why the [illegible]

leaves are dull-grey in colour, have a thick and waxy cuticle or develop a dense growth of hair which shade the chlorenchyma. The leaves are thick and small, often stiff and coriaceous (sclerophyllous), [illegible] ased and [illegible] ercellular [illegible] he plants [illegible] he soil is dry or water absorption slow, due to poor root development or low soil temperature, as in many alpine plants. Here a combination of low atmospheric pressure and intense illumination results in water loss which far exceeds absorption. Plants growing in soils with deficient aeration, excess of acids or alkalies or those growing in very dry, exposed situations, such as deserts, have similar structural peculiarities. In the deserts, the soil is dry and absorption difficult, and dry air and strong illumination promote excessive water loss.

Plants growing in weak light or in shade also show many struc- [illegible]

tissues almost lacking. Branches are few and leaves fail to expand and sometimes remain scaly. The palisade is lacking. Stems are succulent and roots poorly developed. In plants growing in shade,

leaves are comparatively thin but large and broad and have a [illegible] ical tissues are not well-differentiated. The leaves which, are soft and succulent, reach their maximum expansion and the plants their maximum height under conditions of parital shade. The roots are moderate sized.

Reduc[illegible] of structu[illegible] spring anc[illegible] crops, such as cabbage, lettuce, and tea are grown under artificial shade. Such artificial shading produces large leaves of tobacco needed for cigar wrappers

Intense light favours or is actually necessary for the formation of flowers, fruits and seeds. Light is, therefore, necessary for the spread of [illegible] very intense. In [illegible] he highest yield in regions with high [illegible] eas the world's greatest granaries [illegible] re in regions where the percentage [illegible] wet and cloudy years, the yield [illegible] reduced. This also explains why trees in an open community fruit more prolifically than those forming a closed community, where overtopped individuals rarely produce a seed crop.

The quality of light is modified by clouds and fog. Water vapour absorbs infra red light, and from water-surface blue and green rays are mostly reflected or transmitted so that bodies of water appear blue or greenish blue. Red rays induce a great development of tissues and cause the cells to elongate very much. Blue-violet rays, on the other hand, inhibit growth and keep the cells small. Ultra-violet rays [illegible] are responsible for the develop- [illegible] alpine plants.

Different species of plants vary in their demands for light or in their tolerance of shade. Certain plants, *e.g.*, yew (*Taxus*), fir (*Abies*) and spruce (*Picea*) can survive, grow and develop in shade and are

called "tolerant species." There are others that demand light, *e.g.*, sunflower, poplars, willows and pines. They are called "intolerant species". In general, the intolerant trees have an open crown and their foliage is thin, being profuse near the ends of branches. In the forest, their lower leaves and branches die and fall and the trees grow straight and slender. Their seedlings fail to establish if there is shade. If they succeed, their growth is very slow but increases rapidly when from one reason or another light becomes available. The tolerant trees have a dense growth of leaves since leaves develop also on the interior of the crown. They retain their branches and the stem is thick in proportion to its height. Their seedlings tolerate the deep shade and continue growing slowly for many years. When the old trees die and light reaches them, they make rapid development.

The ground flora under the deep shade of a dense forest is very poor, consisting only of low herbs. These herbs show maximum growth in spring and early summer before the new leaves appear on the trees. Under such conditions, intolerant plants cannot establish and only seedlings of tolerant trees can grow.

A knowledge of tolerance is especially important in forest management. As the conditions on the forest floor are unfavourable for the seedlings of intolerant species, the forest finally comes to be inhabited by the tolerant species. To promote the growth of less *tolerant tree species, the tolerant trees have often to be removed.*

Many plants are affected in a significant way by the length of the daily period of illumination. **Photoperiodism***, as this effect of light is called, explains why long-day garden plants, which are grown for vegetative parts develop best in spring and late fall. The differences in photoperiodic response between varieties may be the sole reason for success or failure of a crop at a particular latitude. Flowering shrubs and herbs too, if grown beyond their usual latitudes, may be pampered and kept alive but they often fail to flower because the length of day is unsuitable, or may invariably flower too early in the spring or too late in the fall.

In evergreen woody plants the cessation of growth and subs[illegible] "hardening" occur in response to length of day. *Among* [illegible] growing within range of street lamps, some winter-[illegible] place. Street trees of several species retain their lea[illegible] illuminated by street lamps long after dormancy [illegible]

*Here only the ecological aspect of photoperiodi[illegible] For a more detailed and academic account of the [illegible] *Plant Physiology*' (10th edition, 1970) by the author.

fall on the opposite side. Every winter, frost injury results in suc plants because they do not go into complete dormancy.

Commercial green-houses make use of supplementary lighting an controlled period of illumination to bring crops into flowers f special days or to produce maximum vegetative growth. Growing crop for its vegetative parts in one latitude for which seeds must b produced in another latitude is now not an uncommon practice.

Photoperiodism is characterised by great ecological significanc It explains why many plants in the tropics ... here the light period why ... It is ... rare ... tem ... Species requiring hig ... days to mature are definitely limited in the northern range.

The formation of abscission layers in leaves, preceding their fal and the accompanying decline in physiological activity may initiated in response to shortening days, regardless of reduction temperature or age of the leaf. Therefore, at or beyond the norther limits of their range, trees may be killed by frost because they a not yet sufficiently dormant to withstand low temperatures whe they occur.

It should not be assumed that plant distribution is primari determined by the length of day Many species are little affected by Also, temperatures, especially at night, modify periodic requiremer and responses in several species The initiation of cambial activ which occurs in springs every year suggests a photoperiodic respon It is probably the result of interaction of light and temperatur Photoperiodism is just another factor which may operate w temperature, moisture and light to determine the range and distrib tion of species.

TOPOGRAPHIC FACTORS

A considerable part of the plant grows inside the earth, th environment of which also affects the life of the plant. The facto of the earth are of two kinds : those that relate to the form ar surface behaviour of the earth and those that relate to the structu and composition of the soil. The former ... mou ... bring ... large climate zones

also by modifying the edaphic factors.

1. **Altitude**. The effect of altitude is best seen in mountains. ... ly cooler. ... variation ... enveloped ... r time the weather may be clear and extremely dry. With the increase in altitude, the vegetation also changes. In going up a mountain one comes across the same zones of vegetation as are met with in moving from the equator towards the poles. The sequence of vegetation illustrated in figure 1.1 would be evident to any one who makes a journey up the Western Himalayas.

In high mountains, increased insolation favours flower formation. The greatest abundance of flowers is met with in the alpine meadows.

2. **Slope.** The effect of slope on insolation has already been mentioned (page 11). In the mountains, the south-facing slopes are sunnier and warmer than the north-facing slopes.

Slope affects the amount of water in the soil and on its surface, and determines the character of the soil. On a sloping soil, water flows down before it had time to soak into the soil. The amount of rainfall lost by run off increases with the steepness of the soil and the water absorbed correspondingly decreases. In spite of heavy rainfall a sloping soil is usually dry and its surface unstable on which plants are unable to establish themselves firmly. On the steep slopes of the Western Himalayas such xerophytic plants as agave and arboreous species of *Euphorbia* are often met with

On soil that is level or almost so, new soil is formed by weathering and humus also accumulates. On a sloping soil, this material is carried down by the rapidly flowing rain water and is deposited in the valleys below or at the river mouths where it forms mud flats. On steep slopes even in regions of heavy rainfall active erosion and denudation due to this moving surface water may result in an almost entire absence of higher plants from considerable areas on hill side.

Slope also affects the position of the water table, *i e*. the level below which liquid water collects. In general, the water table is nearer the soil level in valleys than in hills. This makes water easily available to the plants in the valleys which are usually covered with luxuriant vegetation.

3. **Exposure.** Exposure of slope largely determines the type of vegetation. A slope exposed to sun and wind bears vegetation entirely

different from that which is less exposed to either. The southern slopes of the Himalayas bear a more mesophilous and the northern slopes a more xerophilous vegetation, because the former come in the way of the monsoon winds and are humid whereas the latter are dry due to dry winds.

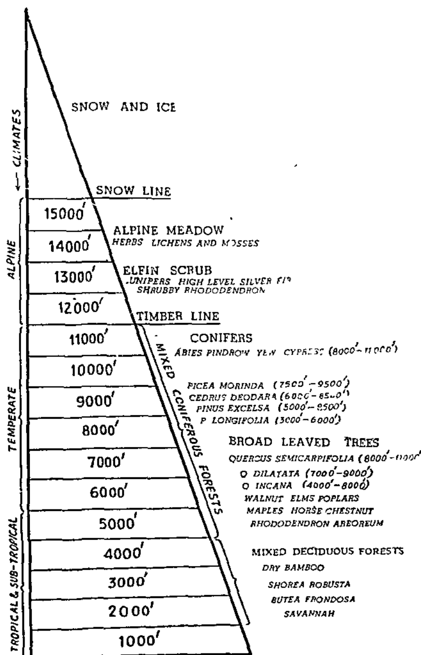


Fig. 1.1. Altitudinal zones of vegetation in the Western Himalayas

4. **Direction of Mountain Chains.** Mountains affect climate. They steer winds into definite direction, occasion winds, cause rains on certain sides, and condense water vapour in the form of clouds and fog. Thus, the Eastern Himalayas turn a part of the summer monsoons towards Uttar Pradesh and Punjab. The outer Himalayas are clad with luxuriant forests and the middle and inner Himalayas are dry because the moisture in the winds is condensed and deposited before the interior is reached. Thus, in the Kulu Valley on the southern side of the Rohtang Pass (12,000 feet above sea level, and source of the river Beas) there is plenty of rain and the hill-sides are covered with luxuriant forests. When you cross the snow-covered peak of the Rohtang Pass you go down into the Lahul Valley, which is intensely dry and plants are few both in number and in variety.

QUESTIONS

1. How would you define plant ecology ? What are its branches and their fields ?
2. Explain the following terms :
   Environment ; Habitat ; Ecological factors : Epharmony.
3. Name and classify the several factors of the environment that determine the distribution of plants.
4. Distinguish between direct and indirect ecological factors, giving suitable examples What is meant by the interaction of factors ?
5. Explain the following terms :
   Saturation deficit ; Relative humidity ; Thermal constant ; vapour pressure deficit.
6. Describe the effect of temperature on the distribution of plants. What is Schimper's Law in this respect ?
7. Explain Schimper's Law relating to the distribution of vegetation types.
8. Compare the structural peculiarities of sun and shade-plants.
9. What is the effect of light on the structure and distribution of plants ? Under what conditions of illumination would the following plants give the maximum yield ?
   Wheat ; Tea ; Cabbage ; Orange.
10. How does increase in altitude affect vegetation ? Illustrate your answer with reference to the vegetation of any mountain that you have visited.
11. What is the ecological significance of photoperiodism ?
12. How does moisture content of the atmosphere affect plants ?

THE ENVIRONMENT *(Contd.)*

EDAPHIC FACTORS—THE SOIL

Soil is the top cover of the earth in which plants can grow. It is a complex composite mass which consists of weathered rock material mixed with decomposed organic matter derived from the remains of plants and animals.

With the exception of stem parasites and epiphytes, nearly all the higher plants are anchored in the soil and obtain from it their mineral nutrition and water supply. The principal components of the soil are the mineral particles derived from the rocks. Rocks occur at varying depths beneath the surface of the earth or in some cases they are exposed as in the mountain slopes or where the earth has been cut for highways or railroads, on stream banks or in quarries. A rock [illegible] hard rocks are [illegible] particles [illegible] of rocks [illegible] proceeding. Several natural forces have contributed to the breaking of rocks into smaller fragments These forces are : the moving glaciers, fast running water, winds, temperature changes, frost and chemical action of atmospheric gases. The roots of plants, and the [illegible] that grow on rocks also contribute towards this [illegible]

[illegible] ing the rainy season must have observed fast-moving water flowing down the slopes after a heavy rain. The water flows down in streams at first. Later, the small streams join and form larger streams. As the amount of water increases, it catches up speed. The swift-moving water is

accompanied by great noise which is produced by the water striking against the rocks and by the stones and pebbles that the water carries with it. These pieces of stones have been torn asunder by the hurtling waters from the larger rocks. The water does not merely carry a stone or a rock piece. It batters and grinds it with other rocks and pebbles, wearing away its sharp edges and breaking it into smaller pieces until it may finally be a rock or a pebble no more, but only a powder as fine as flour. Under the grinding mill of running water, the huge rocks are slowly but surely being converted into a fine powder.

Moving glacial ice sheets have enormous power. When they move through the bedrocks, they move even the large rocks, tearing, shattering and grinding them, often to the fineness of powder. Avalanches of huge ice masses in the mountains in their precipitate ... carry them along at high speed. ... another and against other rocks are shattered to smaller pieces. Winds make a similar contribution. The smaller and lighter rock particles are blown about at high speed and, striking against one another and against the large rocks, are made finer still.

Frost followed by thawing is another rock-weathering agency. ... like the lichens and the roots of plants growing in cracks and crevices.

The mere grinding of rock material into finer particles does not produce a soil. These rock particles are subjected to the hydrolytic action of water and the solvent action of atmospheric gases, especially carbon dioxide and oxygen. The rock materials ...

mixture of rock particles and humus is the fully developed soil. The dead remains of plants and animals regenerate life by making the soil fit for plant growth. One essential difference between a fertile soil and a mere mass of rock-fragments lies in the organic content of the former.

The weathering and humust-forming processes (due to fungi and bacteria) are more active near the superficial layer of the earth and become progressively less active in the lower layers. Consequently, the appearance and composition of the soil change from the surface downwards. A cross-section of the soil, as seen in a trench, is called **soil profile** (Fig. 2.1). The soil profile shows more or less distinct layers or horizons which differ in thickness and character as one goes from the surface downwards. The uppermost layer is called the **A-horizon.** This is the topsoil in which crops grow. It develops as a result of the combined effects of weathering and the activities of living organisms and is rich in humus. The thickness of the topsoil varies from a mere film to about 10 feet. It is usually dark brown in colour. Ordinarily, four feet of this topsoil are necessary for growing food crops, fibre plants which furnish material for making cloth, and trees from which we get timber for building and furniture.

Under the topsoil is the **subsoil,** known to soil scientists as the **B-horizon.** The sub-soil is usually of a brown colour, lighter than the topsoil. It is made up of decomposing rock material, to which have been added many of the soluble minerals and the finer rock particles which have been carried down by water seeping down through the soil. It is more closely packed than the topsoil and is largely devoid of life. It serves as a reservoir of water. The rainwater that soaks down accumulates in subsoil. This water later rises

material into which the
is is called the **C-horizon**
ie nature of soil profile
on than on the parent
Usually, the topsoil is
ces devoid of vegetation
or with a poor plant growth may have no topsoil, and the subsoil then extends to the surface. In such situations the profile has only a single layer.

A true soil, then, is made up of inorganic and organic components, air and water containing dissolved substances. Micro-organisms, both plants and animals, are also present in it. The relative proportion of the various components varies greatly and depends

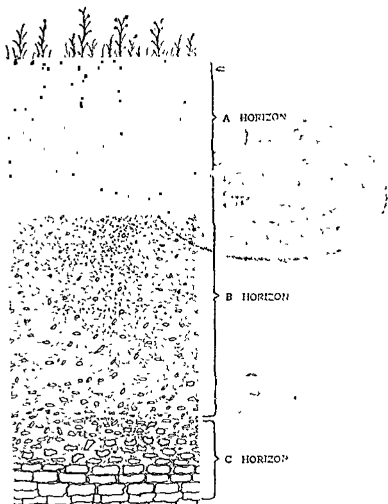


Fig. 2.1. A soil profile

upon the nature of the soil, its depth and the state of its irrigation. Ignoring for the present the living organisms, an average garden soil has the following composition :

Mineral matter	=40% by volume
Organic matter	=10% by volume
Water	=25% by volume
Air	=25% by volume

These constituents of the soil show great local quantitative and qualitative variations and constitute **edaphic factors.**

1. Mineral Component and Soil Texture. The mineral matter, as already stated, is derived from the rocks. The rock particles differ greatly in size and are classified as on the next page.

Diameter of Particles in mm	Designation	Percentage found in typical		
		Sandy loan	Clay loan	Clay
2 00 upwards	Gravel	—	—	—
2·00 0 20	Coarse sand	65	30	2
0 20—0 02	Fine sand	20	30	9
0·02—0 002	Silt	5	20	25
Below 0 002	Clay	10	20	65

The larger soil particles, that is gravel and sand, have the same chemical composition as the parent rocks from which they are derived and are chemically inert. Clay particles have a characteristic chemical composition being made up primarily of oxides of aluminium and silicon. These and other minerals form a combination which is peculiar to clay. The relative proportion of rock particles of different sizes determines the texture of the soil and affects the plants which grow in it.

On the basis of the texture, soils are usually classified as gravel, sand, loam, silt and clay with various intergradations, such as sandy loam, silt loam. Soils in which the mineral matter consists mainly of sand particles are called **sandy soils** and those that consist mainly of clay particles are called **clayey soils** Sandy soils have little water-absorbing properties and are loose, dry and poor in solutes. The interspaces between the sand particles are, however, large so that water and air can move freely. The clay particles are mostly of colloidal dimensions and possess high water-holding properties, and high plasticity or stickiness Clay swells up when moist and shrinks when dry. This shrinkage is accompanied by soil cracking which often causes great damage to the plant roots. Clay particles have small interspace between them so that neither water nor air can move freely. Such soils readily become waterlogged and are not suitable for plant growth. Air which is essential for the respiration and activity of roots is not available so that water absorption is greatly retarded. An important cha [illegible] negatively charged. On t [illegible] cir surface positively charged [illegible] ese bound cations are exchangeable and are released by other cations like hydrogen and ammonium ions. Unless so released they are firmly

held by the clay particles and are not easily leached by rain water. They are an important source of mineral nutrition of plants. They

and calcium in the soil is a factor of great importance in plant nutrition. Fine sands and silt are intermediate in some of the properties of coarse sand and clay and the proportion of silt present has important effects on soil properties. A soil in which the

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particles (sand) are large and function as individuals and counteract some of the unfavourable properties of clay. The smaller particles form a nucleus around which still smaller particles aggregate to form large, compound particles or granules, a process called flocculation. These large particles of a crumbly soil have large interspaces through which excess water is readily drained away so that they become filled with air. Adequate soil aeration is essential for root respiration. The smaller particles, with their small interspaces, retard the movement of water and air, and retain moisture. Hence, loam soils have a higher and a more uniform water content than sands. As a result of aggregation the soil combines the water-retaining properties of clay particles with the aerating properties of large particles. This increases the productivity of the soil. Aggregation of the smallest soil particles into crumbs, therefore, is a matter of very great importance in agric

compact and

for optimal r

Moreover, the clay component of a loam soil is rich in exchangeable cations which are bound on the surface of its particles and which are so important in the mineral nutrition of plants.

2. **Soil Humus.** Humus comprises the dead organic matter of the soil derived mainly from the decay of the dead remains of plants and plant parts. It is one of the most important constituents of the soil. The decay of organic matter is brought about by bacteria, fungi and protozoa. Plant structures like stem, root, leaves etc. are converted by these soil micro-organisms into a dark-coloured amorphous substance in which the parent plant structures are not

recognisable The term humus is applied to this part of the soil organic matter. Dead animal matter and animal excreta in process of decay also contribute to its formation. Earthworms also play an important part in the formation of humus by dragging dead leaves into their burrows.

Humus occurs in the soil in all stages of decomposition and has no definite chemical composition since it is always changing. In humus formation the nitrogen calcium, potassium and other minerals bound up in the dead plant and animal remains are changed into soluble compounds in which form they can be again absorbed by the living plants. Humus is in fact one of the most important sources of necessary nutrients, especially nitrogen, for the majority of plants Its rapid formation adds to the fertility of the soil

Humus is dark in colour, light in weight and more or less intimately mixed with other soil components. It greatly improves the physical condition of the soil which in turn controls to a very great extent the supplies of water and air to the roots. It acts as a weak cement which binds sand and clay particles in the form of tiny balls called "aggregates". These range from the size of a pinhead to that of a pea. These give to the soil a crumbly consistency and prevent it from packing in a solid mass. Humus makes the soil porous by separating the clay particles. This increases aeration and percolation of water and its absorption by the soil. In such a soil roots readily penetrate and bacterial activity increases. In its last stage of decay humus occurs in colloidal state and together with clay forms the colloidal complex of the soil. Humus possesses great water-holding properties, which greatly exceed that of clay. It, therefore, greatly increases the water-holding capacity of sandy soils. On this account, soils rich in humus can support good vegetation even in regions of moderate rainfall. Soils that are poor in humus are hard, easily crack and expose great surfaces to evaporation. If such soils also have a low clay content, a rapid loss of water and leaching of soluble salts take place. This makes the soils dry, poor in minerals and unproductive. Humus is thus a reservoir of nutrients, of oxygen which is necessary for root respiration, and of water. Humus accumulation is usually a very slow process. It must, therefore, be maintained with great care if our soils are to continue to be productive. It is always limited to the upper layers of the soil and these are the very layers that support plant life. The formation of humus depends upon a number of factors, the most important being the presence of plant and animal remains, suitable bacteria of decay and suitable

soil conditions. It is most rapid in warm, moist and aerated soils *which offer most favourable conditions for the growth of fungi and* bacteria of decay.

In the forests, raw humus occurs in three distinct stages of decomposition. The forest floor is covered by organic matter which is slightly or not at all decomposed. This comprises **litter**. Beneath it is a layer of partially decomposed organic matter called **duff**. Still deeper, the decomposition of organic matter has progressed further so that it has lost its original form altogether. This deeper layer is called **leaf mould**. Under anaerobic conditions, such as exist in water-logged soils, organisms causing decay are excluded and plant bodies accumulate as peat, and humus formation is retarded.

3. **Soil Organisms.** Soil microorganisms, plants and animals, are an important part of the underground environment of the plant. There are numerous species of bacteria, fungi and protozoa that inhabit the superficial layers of well aerated soils that are rich in humus. The organic matter contained in dead plants is necessary for their nutrition. They decompose this organic matter and convert it into humus from which other plants derive their nutrition. There is thus a close relationship between vegetation and the soil organisms. The latter are also responsible for removing from the soil the debris resulting from the death of previous generations of plants and animals and also for the production in the soil of simple materials which are necessary for the growth of vegetation. But for the decay-causing activity of these universal scavengers of nature, which change the dead vegetation into useful compounds, the earth would be filled with the dead

M s.

The [illegible] y would germinate, would not develop into mature plants unless the spores of a suitable mycorrhizal fungus are present in the soil. The

on to the plants.

Bacteria are very useful and the most numerous inhabitants of the soil. Besides those that bring about decay and fermentation are the nitrogen-fixing, ammonifying and nitrifying bacteria found in all well-aerated soils that contain humus and the denitrifying bacteria which flourish in soils from which air is excluded.

Large amounts of nitrogen and minerals in the soil are by the micro-organisms that produced them from plant

are thus saved from leaching. Upon their death and decay these substances are released and again utilised by the higher plants.

Some of the larger animals living in the soil play an important part in improving soil conditions for agriculture. The earthworms cultivate the soil and bring deep soil to the surface. They consume large quantities of soil, digesting nutritious matter from it as it passes through their intestines. In this process the soil is mixed up and the coarse soil particles are crushed into finer particles as if by a grinding mill The residue of the soil, together with their nitrogenous waste, are deposited on the surface of the ground as "worm castings". The burrows of earthworms improve the aeration and drainage of the soil. Moles injure plant roots and are harmful.

4. Soil Water. Great quantities of water are retained in the soil. The amount varies in different soils. Its amount in ordinary garden soil is about 25 per cent by volume. The chief source of soil water is rain. After a heavy rainfall some of the water drains away along the slopes. This is called the **run-away water** and is not available to the plants. Some of the water percolates downwards through the large pores between the soil particles under the influence of gravity until it reaches the water table. This is called the **gravitational water.** Although readily available to the plants, the gravitational water is seldom present long enough to contribute much to plant growth. The whole of it usually drains out of at least the upper horizon of the soil within a day or two. If it remains longer in the soil, serious injury to root systems may result from lack of oxygen and accumulation of excess carbon dioxide. Obviously, therefore, gravitational water is of little direct value to plants and may even be injurious.

Much of the rain water is, however, retained by the soil particles against the force of gravity and makes the soil wet. Some of this water is absorbed by the soil colloids and is held tightly by them. The soil colloids are of great significance as water retainers. When the soil is dry, these colloids can absorb small quantities of moisture from the atmosphere. The water thus absorbed by them is called **hygroscopic water.** It is held very tenaciously by the soil colloids and is non-available to the plants. Even air-dry soil contains an appreciable amount of hygroscopic water. The amount of water, expressed as a percentage of the dry weight, that a 1 mm. thick layer of soil can take up from an approximately saturated atmosphere at a constant temperature is termed the **hygroscopic coefficient** of the soil. A small amount of water is bound to the molecules of some soil minerals by strong chemical bonds. This chemically combined water does not yield to the absorptive forces of the root. The

remainder of the water fills the spaces between the non colloidal soil particles or forms films round them. This is called **capillary water** and is of the greatest importance to the plant because it is this water that is readily absorbed by the roots. Some water also occurs in the soil atmosphere in the form of water vapour. This probably is not used directly by the plants.

Many terms are currently employed to denote the moisture content of soil and there is some confusion in their use. The hygroscopic and capillary waters together represent the **maximum water holding capacity** of the soil. It is the amount of water held by a saturated soil and may be measured by weighing a unit volume of soil before and after it has been immersed in water for 24 to 48 hours. **Field capacity** is the total amount of water that a soil retains after the gravitational water has been drained away. Soils in the field attain this condition within 1 to 5 days after rain except when the water table is near the surface, or saturation extends to a depth of many feet. The value of field capacity for different soils and at different soil horizons is determined by a number of factors, the most important being *soil texture or size of particles, soil structure, i.e.,* the arrangement and compactness of the particles, and the amount of soil colloids. The greater the proportion of the colloidal complex of the soil, the greater is the amount of water retained by it. Thus, coarse sand may retain only about 10 per cent of its dry weight of water while a loam soil may retain 35 per cent or more, and the water-holding capacity of clayey soil is still higher. Soil moisture values are usually expressed in terms of volume. Another term that is commonly used in ecological studies is **moisture equivalent.** It is the water content of soil after it has been subjected for 30 minutes to a centrifugal force of 1,000 times gravity.

Not all the water present in the soil is available to the plants. The water that can be absorbed [illegible] Normally, it is the capillary w[illegible] and the wilting coefficient. [illegible] that which is [illegible] in associa- [illegible] ich contains [illegible] yield water to plants.

According to another terminology, the total water present in the soil is called holard. Of this the amount that the plant can a[illegible]

The behaviour of the plant is determined by the chresard and not by the holard The holard, chresard and echard differ for different soils For example, the value of echard for a clay loam with a water-retaining capacity of 35 per cent may be 10 while its value for a sandy soil with a water-retaining capacity of 12 per cent may be as low as 1 per cent. It is because the sandy soils yield most of their water that plants often seem to get along well in them. The values of chresard and echard are also determined by the nature and distribution of the root system depending upon the plant species Some plants can absorb more water from a given soil than others. This explains the importance of determining the echard for particular species.

A knowledge of soil water relationship is of great importance in all ecological studies. A term that is frequently used in such studies is the wilting coefficient of the soil. This is the percentage of moisture that is left in the soil at the time whe[illegible] nently. This primarily depends on tl[illegible] higher than the hygroscopic coefficient.. The relation between the two is expressed by the following equation :

$$\text{Wilting coefficient} = \frac{\text{Hygroscopic coefficient}}{0.68}$$

Wilting coefficient is also related to moisture equivalent as follows :

$$\text{Wilting coefficient} = \frac{\text{Moisture equivalent}}{1.84 \pm 0.013}$$

The soil water contains a number of mineral substances in dilute solution so that the soil water should in reality be spoken of as "soil solution."

5 **Soil Air.** Soil that is not water-logged contains air. Soil is a porous structure and the interspaces between the soil particles are normally filled partly by air and partly by water. The amount of air in the soil is determined by the pore size of the soil. Soil air is essential for the respiration of soil micro-organisms and underground parts of plants. Compared to atmospheric air it is slightly poorer in oxygen and richer in carbon dioxide. This is due to the respiratory activity of the roots and soil flora and fauna.

The oxygen present in the soil air is an important factor in soil fertility. It is necessary for the breaking down of insoluble minerals into soluble salts and also in the process of humus formation in which the nutrient material locked up in plant and animal remains is changed into soluble compounds. Oxygen is also essential for bacterial nitrification and nitrogen fixation. It is also necessary for

earthworms and other soil organisms whose activity increases soil fertility. Seed germination, root growth, development of root hairs and absorption by roots all require oxygen. In its absence, these activities are slowed down and ultimately cease.

Oxygen being very slightly soluble in water, water-logged soils are deficient in oxygen and there is an excess of carbon dioxide. Under such conditions, the anaerobic respiration of plant roots and micro-organisms results in the production of toxins that are harmful to plant-growth. Nitrifying bacteria are excluded from such soils which are, therefore, poor in nitrate. Well aerated soils are usually free from toxic substances.

Plants growing in water have an extensive system of air spaces In such habitats the algae play a significant role in supplying oxygen to submerged roots. They are of great ecological importance in rice fields, being valuable for root aeration.

More water in the soil means less air. In irrigation, sometimes more water is used than is best for crop production. This reduces the amount of soil air which is also essential. A compromise between the two needs of plants is, therefore, necessary. Water should be applied in such a way as to cause least interference with soil air. When, as a result of irrigation, the soil is saturated with water for any length of time, many seedlings and plants wilt with the result that the crop yield is poor.

6. **Soil Temperature** Soil temperature has a significant effect on plants, especially in cold regions. Functional activity of the root decreases as the temperature falls below a certain optimum. If the soil temperature falls below a certain minimum, water absorption ceases and the plant wilts even though the soil is saturated with moisture. Such cold soils are said to be physiologically dry. The aerial parts of the plant can endure much lower temperatures than the roots. This is of siginficance on mountain tops where the soil temperature is higher than that of the air.

Low soil temperature induces nanism (dwarf size). This explains the dwaf growth prevailing in sub-glacial vegetation. Cold soils favour prostrate shoots and rosette-like growths, whereas warm soil brings forth slender, tall plants

Soil temperature also affects the activity of micro-organisms. The useful bacteria, such as those concerned in the decomposition of organic matter, nitrification and nitrogen fixation all require favourable temperature conditions.

7. **Acid Soils.** Soil reaction also affects the plant. The reaction of the soil is due to the soil solutions. This reaction is acidic or

alkaline acc kcording as the hydrogen ions or hydroxyl ions are in greater concentration. This is expressed in terms of pH value. Water is neutral and has a pH value of 7. Any value below 7 indicates acidity while any value above 7 indicates alkalinity.

There are several causes of soil acidity. In humid regions, where rainfall is heavy, a continued washing away and leaching of the soluble bases like calcium, magnesium, potassium and sodium ions takes place. This leaves behind the insoluble acid residues which accumulate and make the soil acidic. Continual removal of lime and other base elements by plants and the accumulation of acids contained in certain manures (particularly ammonium sulphate) also make the soil acidic Acidity is also caused if soils develop from acid rocks.

Most of the plants grow best in soils that are neutral or only slightly acidic. Certain plants like *Rumex sp.* can tolerate acid conditions while a few others would grow in acid soils. Thus, *Rhododendron* grows best in acidic soils. Acid soils are usually deficient in calcium and the plants growing on them are described as *calciphobous* (Lime-fearing). Plants that are intolerant of acid conditions are described as *calciphilous* (Lime-loving).

Most of the crop plants and vegetables are injured when grown on acid soils. Wheat, barley, sorghum (jowar), tobacco, sugar beet, cabbage, cauliflower, carrots, pumpkin, cucumber, lettuce, spinach, onion, egg plant, chillies and lady's finger fall in this category. On the other hand, certain crops such as rice, oats, rye, buckwheat, maize, cotton, peas, beans, groundnut, soyabean, white clover, castor potatoes, sweet potato, tomato, turnips, radish, strawberry, grapes and water melons tolerate acidity fairly well. Soil acidity exceeding a particular limit is injurious to plant growth. The harmful effect of soil acidity has been attributed to many causes. Acidity checks the activities of nitrifying and nitrogen-fixing bacteria. It is also injurious to earthworms. In acidic soils normal decay of humus is prevented and carbon dioxide and other toxic substances accumulate Plants living in acidic soils usually have endotrophic mycorrhiza, *e g*, *Rhododendron*. It appears that in their case the acidic condition is required by the fungus rather than the plant. Acidity adversely affects the solubility of salts and minerals like phosphate, magnesium, calcium, iron and manganese and thus greatly reduces their availability. It also destroys the crumbly structure of the soil and diminishes its aeration and water content.

Soil acidity, if it exceeds the safety limit, must be corrected. The common method consists in adding lime to the soil in the form of

limestone (calcium carbonate), dolomite (calcium carbonate and magnesium carbonate), or burnt lime. Certain fertilizers, such as calcium nitrate, basic slag and calcium cynamide also reduce soil acidity by leaving lime residues in the soil

Liming of soil not only corrrects acidity but also improves response to fertilizers, promotes desirable bacterial activity, improves soil structure and facilitates the growth of green-manure and leguminous cover crops.

An alternative method of improving acid soils consists in growing acid tolerant crops,given above, especially the leguminous crops.

8. Saline and Alkali Soils. In regions of low rainfall and in arid or semi-arid regions, the soluble salts tend to accumulate in the superficial layers of the soil if the drainage is faulty. Salt accumulation also takes place as a result of continued evaporation of saline capillary water or of salt water from sea shore or borders of salt lakes. Soils which contain high concentrations of soluble salts are described as **alkali soils**, irrespective of the reaction of the salts. Of the salts usually present in such soils, carbonates of sodium and potassium have an alkaline reaction. These salts dissolve and disperse organic matter in the soil, giving it a black or dark-brown colour and the soil is known as **black alkali** Other salts present in alkali soils are chlorides, sulphates and nitrates of sodium, potassium and magnesium. All of these have a neutral reaction and soils rich in any of these salts are designated as truly saline soils. The term **white alkali** is used for such soils on account of the white incrustation which these salts usually produce on the surface.

Sometimes, salts accumulate in the bottom layers of the soil profile. This usually does not produce saline or alkali soils. When, however, irrigation is practised or the ground water rises to the surface and evaporates into the air, a high concentration of the salts is left on the soil and patches of alkali soils are then met with on the ground. Instances of this phenomenon are quite common in Punjab, Uttar Pradesh and Rajasthan.

Saline and alkali soils occupy more than two million acres in Uttar Pradesh where they are locally known as *usar* or *reh*. Considerable areas of such soils occur also in Punjab and are called *kallar* or *thur* and the black alkali soils are called *Bara* Such soils are characterised by a hard and impregnable surface, a hard *kankar* layer of variable thickness at the surface in the sub-soil and poor drainage.

Saline and alkali soils bear practically no vegetation, because plants cannot absorb water from soils containing excess of soluble

salts even though the soil may have plenty of water. Under such conditions, the root cells may even lose water on account of the high osmotic concentration of the soil solution. This causes the plant to wilt Such soils are, therefore, physiologically dry. Moreover, in soils that have a strongly alkaline reaction some of the essential minerals such as zinc, copper and manganese are precipitated and are no more available to the plant. Soils which are poor in available soil nutrients cannot support plant life

Some species can endure high salt concentration in the soil Thus, *Suaeda fruticosa*, *Salsolo foetida* and *Salicornia* are met with on such soils.

Excessive accumulation of salt in the soil is injurious to the plants Alkali soils, therefore, do not support plant life and are a national waste. To make such soils fit for agriculture it is necessary to remove the accumulated salts. The following methods are adopted for the reclamation of saline and alkali soils :

(*i*) **Mechanical methods** The water table is lowered to five or six feet below the surface by a network of deep cuts at right angles to the slope of the land. The land is then irrigated by good quality water. Considerable quantities of salt thus leach down below the ordinary root zone. Two or three leachings suffice to remove all harmful salts. In the beginning, salt tolerant crops like rice, barley and sugarcane are grown. Sometimes, surface incrustations of alkali are removed with a scraper or a rapidly moving stream of water.

(*ii*) **Chemical methods** Soils that are alkaline are best reclaimed by the addition of gypsum (calcium sulphate). Gypsum reacts with the carbonates of sodium and potassium to form the insoluble calcium carbonate and the sulphates of sodium and potassium. The soluble sulphates can be washed out by heavy irrigation and drainage. Calcium carbonate is removed by adding farmyard manure. Alkalinity is neutralised by the addition of sulphur.

(*iii*) **Growing salt-tolerant plants.** Cultivation of salt-tolerant crops and plants is another method. In this category fall sugar-beet, rice, lucerene, **Patsan**, wild indigo and babul (*Acacia arabica*).

9. **Soil Cover** Soil cover is a factor of great importance. It may be either living or non-living. The latter protects the soil against loss of water and against rapid changes of temperature. In arctic and alpine regions, the soil freezes during winter. This causes the plants to be forced upwards ; their roots more or less break and they may suffer death from loss of water through exposure to air. An efficient soil cover largely prevents this. A covering of snow is

perhaps the most effective of soil covers in protecting low plants from rapid temperature changes.

A covering of dead leaves, fallen twigs and withered grass serves the same function as a covering of snow, though not as effectively. It also retards the movement of runaway water and prevents the washing away of soil by water and its blowing away by wind.

The living cover of the soil consists of vegetation and is of great significance in protecting the soil from wastage and in improving its fertility and texture. Vegetation cover retards the movements of water over the surface of the soil by means of stem and leaves and directs the water into the soil along the roots or old root channels, or openings left by moving earthworms and other organisms. It also helps to keep the soil in place. The more dense the vegetation, the more effective it is in holding the soil in place. The plant roots form a network which tends to hold soil particles together and prevents them from being washed away The trees act like leaky umbrellas. Their leaves prevent rain drops from striking the soil directly. This prevents the pounding effect of rain drops from splashing the soil away. In this respect, litter and leaf mould are also important. The humus formed from decaying plant material absorbs large quantities of water and allows it to soak into the soil, instead of running over its surface. As a result of this slowed down movement, there is reduction in the rate and amount of run-off, and a consequent decrease in the frequency and magnitude of floods and soil erosion. At the same time, a greater percolation and absorption of water renew the water content of the soil and regulate the flow of streams.

While the plant cover takes away from the soil water and minerals, it also adds organic materials and minerals in the form of humus. Humus renders loose soils less erosive, while the nutrients stimulate growth and increase density of cover during the rainy season.

The edaphic factors described above are only of local importance. Their effect on plant distribution is summarised in Schimper's second law which states that the local distribution of plants is determined chiefly by the nature of the soil either directly or in its relation to other factors.

SOIL EROSION

The loss of fertile top soil is called **soil erosion.** The agents that bring about soil erosion are water and wind. Soil erosion by water

is determined by several factors, which include the kind of rainfall, the type of soil cover and the slope of the land. When rain falls on any area from which vegetation has been removed, the dashing rain drops beat upon the soil, make it compact and reduce its absorbing capacity. Rain drops falling on bare unprotected soil surface churn the top soil into thin mud which runs down the slopes and fills up the soil pores and clogs them. The excess water accumulates on the surface and begins to run down the slopes. It is the running off of this surface water that causes erosion and loss of soil. This running water carries with it surface soil particles, the humus and the mineral salts.

The removal of a layer of top soil is called **sheet erosion.** More soil is removed from steep slopes than from gentle ones. Heavy rains cause more loss of soil than do light, long-lasting showers. During a gentle rain, water is able to soak into the soil instead of running off the surface There is more erosion if rain falls on wet soil because running of water starts quickly on soil which is already saturated with water. As more water runs in one place, it runs faster and this gives it added cutting and carrying power. The swift moving water cuts the soil deep, forming ravine and also tears down larger pieces of the bank. This kind of soil erosion is called **gullying.** The richest portion of the soil is thus removed leaving exposed a hard, compact, poor absorbing surface. Besides causing erosion, the running water destroys the remaining plant cover. Soil removed from the uplands causes great destruction in silting over vegetations of adjoining lowlands. This is what happened in Punjab and several other parts of India as a result of unprecedented heavy rains and floods in September 1955.

Vegetation of any kind helps to hold the soil in place and prevents soil erosion. The more dense the vegetation, the more effective it is in holding the soil in place. In the mountains, unplanned and extensive lumbering of forest trees and overgrazing or destruction by fires have a very devastating effect. The soil is removed or its absorbing capacity lessened. Vast areas are thus rendered unfit for agriculture. The great reservoirs of water on the mountains, which are the major source of water for irrigation, are let loose. The water, instead of being released gradually, comes down in the form of destructive floods. Forests and grasslands protect the soil from this kind of erosion. This protective effect is due partly to the above ground parts, partly to humus accumulation and in the main to the binding action of roots and rhizomes. Plant cover also modifies the melting of snow in the mountains. Under the

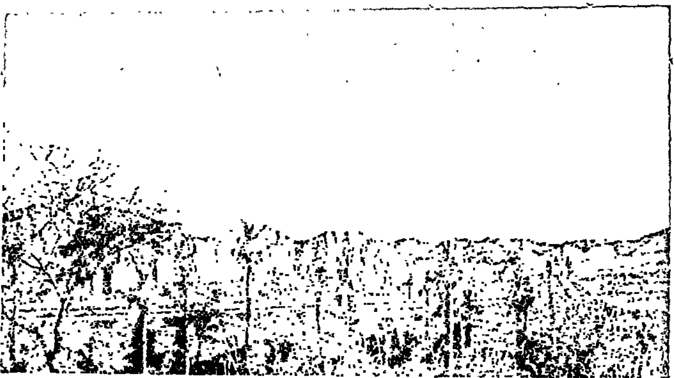


Plate 1. Soil erosion by water at Panchkoola, near Chandigarh on Ambala Kalka road

(*Photograph by B N. Sood*)

Text reference on page 36]

[*To face page 36*

Plate 2 Silting of low land as a result of torrential floods

Text reference on page 38]

Plate 3. An approaching dust storm in the desert

Text reference on page37]



P... : Sand dunes with the sand binder *Saccharum sp.* growing here and there

Text reference page 37-38]

(*Photo by Prof. P.C. Joshi*)

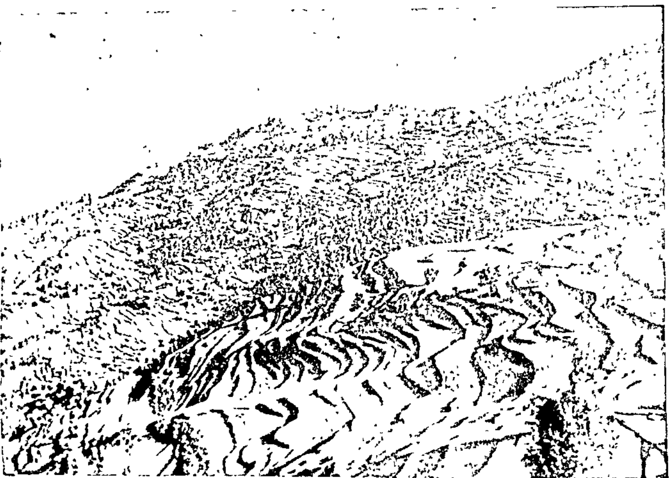


Plate 5. Terraced fields in Simla Hills
Text reference on page 42]

[To face page 37

protection of forest cover, the snow melts gradually after the warm weather sets in. The water moving slowly down the slopes is more apt to be abosrbed, thus, lessening the chances of erosion.

It must be abundantly clear from the above discussion that water which is indispensable for plant life can also be a very destructive agent, if it is not under control. Bare soils, clean cultivated orchard soils, or soils growing cultivated crops such as vegetables, wheat, cotton and tobacco have little protection and suffer greater losses by washing than do soils protected by forests or pastures. A fertile soil that contains all the plant foods and which is in good condition produces a rich crop and gives large yields. The thick crop also helps to protect and hold the soil. Soil in good tilth is open and porous. More water enters such a soil and there is less run off. Water that is absorbed is saved for future use. That which runs off the surface causes erosion. Anything that slows down the flow of water over cultivated fields checks the loss by erosion. It may also be mentioned that soils subject to water erosion are unstable. Plants cannot grow on a soil that is not reasonably stable.

Another agent that causes soil erosion is wind. Wind erosion is a problem in dry areas like Rajasthan, Kutch and the Punjab plains Here the rainfall is scanty and during summer months the surface soil becomes powder dry. Strong winds blow and the finest material on bare soils, especially sandy ones, may be carried away during dust storms. The sand drifts into roads, ditches and on to farms and crops so as to cause untold damage. In some places small buildings are nearly covered with wind-blown soil. Wind erosion is best seen in deserts and along the seashore. Deserts are characterised by shifting sand dunes. Very few plants can grow on such unstable soils. The sand is being constantly blown up from behind and dumped in front so that the dune moves forward. Plants growing in the rear are uprooted or else their roots are exposed to the dry winds. *Plants growing in the path of the dune may be buried* by the wind. Cultivated areas which lie in the path of the wind are covered by sand and are gradually made unfit for plant life. The desert thus moves forward in the direction of the wind. This kind of soil erosion is responsible for the rapid extension of the Rajasthan desert.

In areas of shifting sand, only a few plants known as "sand binders" can grow. By their extensive root development they help to stop the movement of sand. Common examples of such plants in the desert regions are grasses like *Saccharum munja*, *S. spontaneum*, *S. arundinaceum* and *Cynodon dactylon* ; *Calotropis procera*, *Capparis*

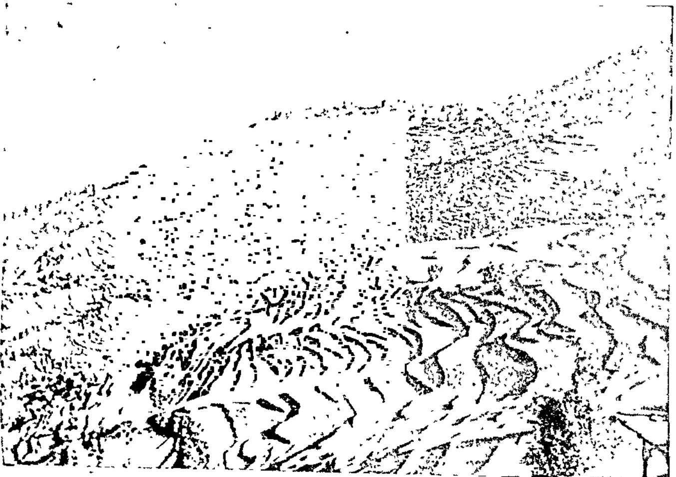


Plate 5. Terraced fields in Simla Hills
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aphylla, Ziziphus nummularia and *Launea udicaulis*. Some of the sea-shore sand-binders are : *Portulaca oleracea, Indigofera cordifolia, Sesbania juncea, Oxalis corniculata, Ageratum connyzoides, Blumea memberanacea, Salvadora oleoides, Datura stramonium, Saccharum spontaneum, Ipomoea pes-coprae (I. biloba), Canavalia Lineata, Spinifex littorius, pandanus tectorius* and species of *Sida*.

The losses due to erosion are enormous. The various factors which aid soil erosion are destruction of forests, overgrazing of grasslands, improper methods of agriculture and destruction of wild life. The normal decomposition of dead animals fertilizes the soil.

SOIL CONSERVATION

Soil is the top cover of the earth in which plants can grow. Four feet of soil are necessary for growing food crops, plants that furnish fibres for making clothing, and trees which furnish the material used in building our shelters. We are completely dependent upon the soil for our basic needs. In fact, soil supports man, animals and all plants living on land. The destruction of fertile top soil by erosion is fraught with gave consequences to mankind. It takes nature 400 to 1,000 years to build one inch of top soil, but a single dust storm can blow it away and a single flood can wash it out to sea. With the loss of the valuable upper layer of the soil are also lost the best guarantees of continued supply of food and lumber. It is, therefore, necessary that the soil should be protected against loss. This is called **soil conservation**. As a result of unchecked soil erosion large area in Africa, China, India and Latin America have been converted into deserts of rock and shifting sand. In India, we inherited one of the richest soils and yet we are not producing enough food for ourselves and our animals. In many other parts of the world also, rich farm lands have changed into waste lands. All the world over, soil losses through erosion are so serious as to threaten mankind with starvation at some time in the future. In the U.S.A. alone it has been estimated that nearly 3 million acres have either been ruined or severely damaged by soil erosion. Uncontrolled soil erosion can lead to national extinction just as certainly as the more rapid and dramatic destruction of modern warfare. Soil conservation is, therefore, not a matter of individual concern alone but is a national problem of the first magnitude.

Soil conservation is concerned with keeping the soil in place, the maintenance of soil fertility and the efficient use of land with a view to establishing a stable, scientific agriculture. The various

methods employed for this purpose aim at keeping the soil protected by close-growing vegetation and maintaining its humus and mineral content. Vegetation cover controls soil erosion by both water and wind. Among the methods used for soil conservation are the replanting of forests and growing grasslands, contour planting, strip cropping, terracing, control of grazing and rotation of crops.

1. **Soil fertility.** On infertile soil plants do not grow well. Such a soil is more exposed to wind and water erosion. Fertility of the soil depends upon its humus content and mineral content. Fertile soils support thrifty crops which protect the soil against wind and water erosion, leave more residue materials in the form of stalks of maize or cotton, potato tops and stubble of wheat, oat or barley These hold and protect the soil and later on when they are ploughed under, they are converted into rich humus by the action of fungi, bacteria and other micro-organisms which bring about their decay. The humus supplies plant nutrients to the crops that follow. It also absorbs water and reduces the rate and amount of run-off and thereby aids in the prevention of soil erosion. Organic matter also increases soil aeration and stimulates the activity of micro-organisms. To maintain a sufficient amount of organic matter in the soil, overgrazing should be avoided.

Plants require a number of mineral elements from the soil. Elements like iron, manganese, copper, boron, zinc and cobalt are needed only in small quantities and most soils are well supplied with them and also with sulphur. Phosphorus, nitrogen and potassium are needed by the plants in relatively large amounts. When crops like wheat, cotton and maize are harvested, these minerals leave the soil which becomes poor in essential nutrients. Since the mineral nutrients in the soil are soluble in water, some of them soak into the subsoil, especially during periods of heavy rainfall, when much water is draining into the subsoil. This process is called **leaching** and occurs to some degree in all soils. Some of the subsoil minerals are returned to the top soil during ploughing.

When the supply of essential mineral nutrients in the soil decreases, the plant cover becomes poorer and poorer. The soil is then more exposed to water and wind erosion, and the top soil is removed. To prevent this, the fertility of the soil must be restored. This can be achieved by the addition of manure and commercial fertilizers like ammonium phosphate, ammonium sulphate, potassium nitrate, rock phosphate or basic slag. Sandy soils require potassium and vegetables require complete fertilizers containing phosphorus, potassium and nitrogen. The loss of soil nutrients has far-reaching

effects. Crop yield is reduced and the crops are of poor quality and deficient in minerals. This adversely affects the health of man and his domestic animals which obtain the minerals necessary for their health from the plants on which they feed.

Legume crops play an important role in maintaining soil fertility. Their cultivation and ploughing-under adds the much needed nitrogen to the soil and helps to keep up the yield of grain and grass crops.

2. **Crop rotation.** Crop rotation is the old practice of growing different crops in regular order on the same area over a period of years. This rest[illegible] the sowing of le[illegible] alfalfa as part c[illegible] nitrogen compounds to the soil. Such crops as cotton, maize, potatoes or other vegetable crops which deplete the soil and are cultivated to leave bare soil (clean-tilled crops) may be grown in the first year; wheat, oats, or other grain crops, the next year; and close-growing, soil-improving crops such as grasses and legumes, the third year. On lands that wash rather easily, grass for several additional years makes a longer and better rotation. Crop rotation [illegible] used with farm manures [illegible] the control of erosion, [illegible]

3 **Control of grazing.** Sheep and cattle eat the green parts of plants. The excessive loss of leaves gradually leads to the starvation of roots and rhizomes which hold down the soil. The surface soil trampled under the hoofs of animals becomes compact so that rain water no longer soaks readily and the ground remains drier than under conditions of undisturbed nature Cropping off the tops of plants prevents them from reseeding themselves. After a period of years the soil becomes weak and the top-soil is easily blown away by wind or washed away by water. It is, therefore, necessary that excessive grazing should be prevented.

4. **Reforestation.** Rapid erosion by water takes place on the steep land of hills. On such soil long-term meadows or pastures give good protection to the soil. Steeper, more easily eroded [illegible] are better [illegible] control- [illegible] that are [illegible] Once well [illegible] ainst erosion. The forest trees build up a thick layer of humus to prevent floods and erosion. Roots of trees and other plants serve as a natural

dam, catching and holding rain water and preventing it from washing away the soil. In forest reserve areas the cutting of timber should be prohibited or controlled. Steps should be taken to prevent forest fires and to check their spread when they occur. Care is also needed to see that insects do not cause too much damage to trees.

Forests are a great national wealth They provide fuelwood timber for construction, and woodpulp for paper, gums, resins, turpentine and allied materials; medicinal materials like myrobalans and quinine; food and shelter for men and animals. They are also important in checking floods and soil erosion. In the past great damage to our forest wealth has been caused by unplanned lumbering by man without the forests being replaced. Forest fires have destroyed millions of acres of valuable forests. This loss of forests has resulted in the loss of crops, wild animals and valuable soil as well.

Fortunately, the Government of India recognised the seriousness of the problems arising out of the uncontrolled destruction of forests and introduced the festival of **Van Mahotsav.** Van Mahotsav is celebrated for one week each in the months of February and July every year. In these weeks trees are planted throughout the country. Planting is done in waste lands and open lands in and around villages and cities. This is planning for the future. New trees will be growing up while old ones are felled. This is a matter in which all of us are directly and vitally concerned and should be interested. Side by side with this, heavily timbered or burnt out forest regions are being replanted. Older trees are cut for timber and paper-pulp so that the smaller trees may grow faster.

Quite often Van Mahotsav is observed merely as an annual ritual without any forethought in planning. Its importance to the nation is forgotten soon after the trees are planted and they are not properly looked after. Hardly 50 per cent of the planted trees survive. More saplings dry up and are lost in rural areas due to lack of after-care than in the big towns and cities. Again, large shady trees are felled to widen roads or to provide new housing sites. Forest trees are recklessly cut down for timber or fuel or to bring more land under cultivation, with the consequent increase in soil erosion.

To serve its useful purpose, Van Mahotsav should be made an integral part of a well-planned countrywide afforestation programme, which should take into account the needs of the various regions. The arid zones, for example, should be planted with heat- and drought-resisting trees to help soil conservation and arrest the march of the desert. Water-logged areas, for example of the Punjab, need

quick-growing plants like eucalyptus which will help in pushing down the level of sub-soil water. Extensive planting of quick-growing trees is also essential for the increased supply of fuel wood. The requirement of the expanding industry has also to be met. For a planned economy, it is desirable to have one-third of the country's total land area of 1.26 million square miles under forest. The area currently under forest is 300,000 square miles. The target can be achieved only through a properly planned afforestation programme

5. **Contour planting.** This is practised on hill slopes. The land is ploughed at right angles to the slope instead of up and down the slope. On sloping soils, the latter is an improper method of cultivation. On such soils, tilling, seeding and harvesting operations on the contour or crosswise have many advantages. It is easier to plough against than up and down the slope. The crosswise depressions left by the plough catch and hold water untill it soaks. The ridges check the flow of rain water straight down the hills so that there is more time for absorption. Up- and down-hill cultivation leads to heavy loss of top soil by sheet erosion and by gullying. When the plants are in rows across the slope, much more water is held by them than if the rows had been up- and down-hill

6. **Contour strip cropping.** If entire slopes are ploughed and planted as one unit, the rain water flows down the entire slope and collects in low places. If the slope is long, the rain water in passing down over the surface becomes faster and soon attains great cutting and carrying power. Heavy rain would cause gullying and severe sheet washing.

Now-a-days, long slopes are broken up into a number of strips laid out across the slope so that crop rows are on level. Strips of dense-growing and soil-covering crops such as alfalfa, grasses and cereals are alternated with clean-tilled crops *i.e.* those that are cultivated to leave bare soil between rows such as maize or potatoes. Some sheet washing does take place but this arrangement checks the momentum of run-off, filters out the soil carried from the tilled areas and increases the absorption of rain water. This prevents gully formation.

7. **Terracing.** The slope is divided into a series of small flat fields called terraces. Each terrace may be further provided with a broad-bottomed channel with a slight slope towards the outlet. These channels break up long slopes into a number of small water sheds. Sometimes, low ridges of soil or rocks are built across sloping fields. These serve as bunds along the contours. The object is to slow down the flow of water and lead it to the sides of the fields where it flows

tute has been established at Jodhpur. The various steps taken to stabilise the shifting sand include (a) growing of green belts by covering the soil with vegetation, (b) improving pasture, (c) keeping the soil rough rather than smooth, (d) strip cropping and seeding crops against the prevailing direction of wind and making furrows across the slope for holding water and (e) laying of avenues of trees, two or three rows deep, on either side of the roads at right angles to the prevailing winds to serve as effective wind-breaks. The main obstacle in the way is the acute scarcity of water. To meet this difficulty a programme of building canals and boring tube wells to supply the much needed water is necessary. The Rajasthan canal is being built which will be fed by water from Bhakra Nangal Dams in the Punjab. More water is expected in the near future from the Beas (Pong) Dam. It is hoped that there will be enough water to quench the thirst of the desert. Success in this tremendous task will not only arrest the march of the desert but will also make millions of acres of arid land fit for agriculture.

BIOTIC FACTORS

The effects of the activities of living organisms constitute biotic factors. These include interactions amongst plants which grow together in a community, between the plants and the local animals and between the plants and soil micro-organisms. The biotic factors also modify the environment. Above all is the influence of man on plants. This is evident in agriculture and forestry where many of his activities end in modifying vegetation and the environmental factors.

An important biotic factor is due to the grazing animals. Grazing by domestic animals affects the grazed plants by causing injury in many ways. Large numbers of plants are removed and many are trampled under foot. The soil is disturbed, its surface layers destroyed and often only the underlying sand is left behind. In a grazing pasture dung-avoiding species disappear, their place being taken by strongly nitrophilous plants. Grazing has caused great damage to forests in India. Grazing is more intense near villages and often the fringes of forests are overgrazed. In the Himalayas, herds of cattle, goats and sheep are taken to the alpine meadows in summer. These eat up most of the plants on the forest floor. The soil is tampled, made compact and hard, and rendered unfit for tree growth. Tree seedlings are either eaten or destroyed. Forest areas, open to cattle are changed to scrub and finally to a treeless grassy area. In

pastures, the removal of grass often leads to the growth of thorny weeds.

Excessive browsing by goats and sheep has laid bare large areas and made them susceptible to erosion. Recognising this danger of soil erosion and the threat to their forests, only a few years ago the Governor of West Pakistan banned by order grazing and pasturing by goats. Camels spare no tree species. Browsing by them and unrestricted grazing is partly responsible for the spread of desert conditions in parts of the Punjab, Delhi and Rajasthan States.

Sambur, nilgai, deer, hare and other wild herbivorous animals also cause damage to plant life. Nilgai feeds on the seedlings of *Shorea robusta* in U.P. ; deer in Assam and Bengal feeds on the tender shoots of many forest trees, notably *Artocarpus chaplasyha, Morus laevigata, Albizzia lebbek, and Pterocarpus marsupium* Large animals like the pigs, bisons and elephants cause extensive damage to forest species by feeding upon the shoots or uprooting seedlings. Rats and monkeys are other enemies of plants.

Cutting, felling and replanting of forest trees are examples of man's reaction on vegetation. Indiscriminate or selective felling of useful trees in the past without providing for their regeneration has changed the pattern of our forests Thus, in the Himalayas, the felling of climax oak forests has resulted in the growth of coniferous forests like that of *Pinus excelsa, Picea morinda* and *Abies webbiana.* In South India, the spread of *Lantana camera* followed upon the clear felling of forests. Similarly, in Assam and Bengal *Eupatorium cdo atum* has rapidly spread in places previously occupied by sal forests.

Forest fires caused by man's activity are responsible for the complete or partial destruction of vegetation. The result is temporary or permanent alteration in the character of vegetation. The shallow rooted plants are completely destroyed and the deep rooted plants or those with underground stems, like some of the grasses, are only temporarily affected. The latter sprout up following the first rains after the fire, and become dominant. The practice of burning forests to clear the ground for agricultural purposes is still practised by backward jungle tribes in some parts of Assam and Madhya Pradesh. Sometimes, spontaneous fires occur which destroy huge forest areas and make the soil unfit for plant growth for many years.

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for the growth of roots or other underground parts is seldom a factor

in competition In a close community, roots invade the zone from which supplies of water and nutrients for other plants are obtained. The foliage of taller plants casts shade on the smaller ones. As a result of competition, more vigorous and better adapted plants become dominant. Others, less vigorous, are suppressed in greater or lesser degree The invasion or entry of individual plants or species into new environments, already occupied, depends upon the ability of the invaders to compete with established species and individuals for the environmental essentials for growth. In a community the dominant species, which is frequently the largest, makes the heaviest demand on the resources of the habitat. Because of this, the nature of the dominant species often indicates the chief operative factors of the habitat, and determines to a great extent the floristic composition of the vegetation growing under them. The taller plants modify the habitat factors of the subordinate species by casting shade, providing shelter from wind, increasing atmospheric humidity and by determining the humus component of the soil.

The nature of the requirements for which plants compete varies in different habitats. In the forest, light is perhaps the most important, whereas in grasslands, deserts and cultivated soils, competition is chiefly for water and minerals. Competition is a process of vital interest from the standpoint of food production. Most cultivated plants could not compete in the wild. Under cultivation, competition is mostly under man's control. The destruction of weeds, for example, eliminates competition for water and light between them and crop plants. The proper spacing of seeds at the time of planting controls competition between plants of the same kind and results in greater yields. Too close sowing reduces yield as a result of competition for water and nutrients. On the other hand, thin planting with the aim of reducing competition, is not necessarily profitable and may not give the maximum yield because the available water, nutrients, and light have not been utilised fully. Competition should be permitted to operate to the extent of taking advantage of all the potentialities of the habitat. In tropical rain forests, water is always abundant add survival depends chiefly upon exposure to light adequate for growth.

The biotic relationship of soil micro-organisms has been discussed in the earlier pages . More interesting instances of biotic influences are the cases of twiners, climbers, epiphytes and parasitic plants and also cases of reciprocal symbiosis in which each partner in the symbiotic relationship derives some benefit from the other, e.g. lichens, and root tubercles of leguminous plants, and the mycorr

and the roots of higher plants.
ts and the flowers that they

factors are not of the same importance as the climatic and physiographic factors. They are rather the biotic modifications or limitations of the latter or their effects.

QUESTIONS

1. What is soil ? Describe the processes leading to soil formation. What is the composition of a good agricultural soil ?
2. Of what use are the following ?
   Mould fungi ; Bacteria of decay ; Nitrogen-fixing bacteria
3. What is humus and why is it desirable in soil ? How can it be maintained in the soil ?
4. Which component of the soil is more valuable, sand or clay ? Give reasons.
5. Describe two ways in which bacteria enrich the soil. How are soil bacteria harmful ?
6. Life on earth would be impossible, were it not for bacteria. Fully explain what is implied in this statement.
7. Describe the water relations of the soil after a heavy rain. Distinguish between available and non-available water
8. Explain the following terms ;
   Hygroscopic water ; Capillary water ; Field capacity ; Wilting coefficient ; Echard
9. What is soil ? How do the different soil strata differ from one another ?
10. Discuss four factors that affect fertility of soils.
11. How are minerals removed from the soil ? How are they returned ?
12. Name three minerals which are needed by plants in largest amounts ? How is their deficiency in the soil removed ?
13. What are acid soils ? Alkali soils ? Describe the effect of such soils on plants.
14. What are alkali soils ? What steps are taken for their reclamation ?
15. What is soil erosion ? What are its causes ?
16. Discuss the various ways by which soil erosion can be controlled.
17. Why are there more floods now than there were a hundred years ago ? How does reforestantion help prevent floods ?
18. What are the advantages of building dams and celebrating Van-Mahotsava ?
19. Where is wind erosion a problem ? What steps would you recommend for its effective control ?

20 How do plants help to prevent soil erosion and increase the amount of nitrates in the soil ?

21 Describe the several reasons for practising crop rotation. Why are leguminous crops such as alfalfa important to crop rotation ?

22 Discuss the effects of biotic factors on plant life.

23 Give some examples of the way in which man's influence has affected plant life

3

ADAPTATION TO WATER

Of all the factors of the environment water is the most important. It is an essential nutrient and a sufficient quantity of it is a vital necessity for all plants. Besides being the major constituent of protoplasm and the cell sap, it forms the solvent in which gases and mineral substances are absorbed by the plants and moved from cell to cell within the plant body. Translocation of food materials and most of the metabolic reactions in the plant body take place in aqueous solution. Water is one of the raw materials in the process of photosynthesis. It keeps the cells and the plant organs in a turgid condition. No growth is possible without water. The [illegible] is largely determined by the [illegible] therefore, no wonder that water is the most important single factor of the environment which has a great influence on plant structure and most of the other environmental factors influence the plant because they have a direct or indirect influence on its water relation. Water also determines to a very great extent the distribution of plants. In general, forests occur in regions where there is adequate rainfall during all seasons of the year, accompanied by a warm vegetative season. In temperate regions, the atmosphere should be moist so that transpiration is reduced, since the trees are always exposed to transpiration and they cannot absorb water from a frozen soil in winter. Grasslands are found in regions characterised by high summer rainfall and low winter rainfall, while deserts occur where there is low rainfall both in winter and summer.

As stated above, the water factor of the environment has a great influence upon the structure of the plant. The water relations

of the plant are determined primarily by two processes, namely absorption from the soil and transpiration. The former depends on the amount of available water in the soil and the latter upon such factors of the climate as humidity, wind, temperature and exposure to solar radiation. The process of transpiration is of significance to the plant because of its cooling effect. Yet the greatest danger to plants comes from too great a loss of water. For normal growth and healthy development, the plant should have a favourable water balance. This means that transpiration should not exceed absorption.

Plants are found growing all over the world in all sorts of conditions with respect to water supply. They live on rocks where supply of water is always a doubtful matter ; others grow on soil which to all appearance is dry ; others grow on the banks of rivers and canals ; and still others are found actually growing in water. Plants growing in these and other habitats are not all alike. They differ from place to place. This is primarily due to the difference in the water relations of the different habitats. Difference in plant forms may be witnessed even in small areas. In a body of water one would find plants which are partly or wholly submerged. These plants are altogether absent from the neighbouring dry land. In like manner the plants inhabiting the dry land are unrepresented in water. This is due to the fact that the plants growing in each of the two habitats are fully adapted to live in that habitat. No plant can exist in both wet and extremely dry situations. Each species flourishes only in those habitats where it finds a suitable water relation.

From the point of view of water relations, environments differ from place to place and so do the plants. There are places where water supply is scanty or (and) the atmospheric conditions are such as greatly enhance the loss of water from the aerial parts. Such an environment is especially characteristic of deserts, alpine peaks and sand hills and is called xeric. Plants inhabiting xeric habitats are called xerophytes. There are places which are entirely under water as in the case of lakes, ponds and other bodies of water. Such habitats are called hydric and the plants inhabiting hydric habitats are called hydrophytes. Between these extremes are places which are characterised by a medium water supply. Habitats, where water is neither so deficient nor in excess, are called mesic, and the plants inhabiting such habitats are called mesophytes. Plants of forests, meadows and cultivated fields belong to this category. These three

groups of plants are sufficiently, though not so sharply, defined and can be more or less readily distinguished from one another. Sometimes we come across plants that are not easy to classify; they cannot be assigned satisfactorily to any one of these three ecological groups. In their case it is convenient to use combinations of these terms such as *xero-mesophyte* (meaning more xeric than a typical mesophyte), *mesoxerophyte* (a little less xeric than a typical xerophyte), *hydro-mesophyte* (somewhat more hydric than a typical mesophyte), etc. There is another group of plants called **tropophytes.** They are typical mesophytes at one time and xerophytes at another time. Such are the deciduous trees of the temperate zones in the Himalayas where conditions are mesic during the warm rainy season when they bear leaves, and xeric during the cold winter months when they are leafless. *Their perennial parts are xerophyllous* and the parts that are present only in the wet season are mesophytic.

XEROPHYTES

As already stated, xerophytes are plants of xeric habitats. Xerism may be the result of inadequate water absorption or excessive transpiration or in more severe cases due to a combination of both these factors. Deficient absorption of water may be due to an actual shortage of water in the soil when the soil is said to be **physically dry** or it may be *due to* the **physiological dryness** *of the* soil. A soil is sai[illegible]
water in the soil [illegible]
This is the case [illegible]
soils and soils ric[illegible]
in the deserts but [illegible]
are all desert plants xeric. Xerophytes will be found in all habitats *where the soil is poor in water and atmospheric conditions* such as promote rapid water loss. T[illegible]
or cliffs or rooted in gravel, in an [illegible]
xerophytes. Similarly, places with l[illegible]
and high evaporation rate are examples of xeric habitats. The same is true of sand hills and dunes where rapid percolation and shifting of the surface soil, accompanied by intense insolation at soil surface combine to induce xeric conditions. The most intense xeric conditions are met with in saline deserts where arid conditions are combined with a soil containing excess of soluble salts which makes water absorption extremely difficult.

In xeric habitats, only those plants can live which can either economise in the use of water or else have the capacity of resisting drought. The xerophytes have met these conditions in a number of ways. There are the ephemerals which live only for a few weeks during the brief spring season. Many of these plants emerge from their seeds in early spring, bear leaves, develop flowers and fruits within a short span of a few weeks when there is enough water in the soil and the air is humid. When the dry season comes, their seeds have already ripened and the plants die. They pass the rest of the time in the form of seeds which are not easily affected by drought. These plants are **drought escaping** rather than drought resisting. The biennials also belong to this category. Their two periods of active life, vegetative and blooming, coincide with the favourable conditions of the environment. In the unfavourable periods their aerial parts die and they remain buried in the soil where they are comparatively safe from the effect of drought.

The second important group of desert xerophytes is that of **succulent plants.** Succulence is an important adaptation to decreased water supply under arid conditions. There is a preponderance of thin-walled parenchyma elements over the thick-walled tissues. The former remain distended and turgid. Low water content causes the conversion of polysaccharides into pentosans which have a high water-binding property. These together with the nitrogenous compounds of the living cells bring about great hydration of the protoplasm that results in succulence

Succulents are of two types, namely stem succulents and leaf succulents. In the first category are the cacti and cactus-like *Euphorbias.* They are characterised by succulent stems with reduced or spine-like leaves. The photosynthetic function of the leaves is taken over by the thick green stem. The stem has a strongly cuticularised epidermis, the stomata are few and mostly closed so that transpiration is greatly reduced. The roots are spread near the soil surface and whenever there is a little rain, the roots rapidly absorb [illegible] soil strata. The water is stored in the wa [illegible] very economically in times su [illegible] ificant loss of water the cacti of [illegible] can live on this stored water for many months or even several years without any external water supply. Since these succulents can endure relatively severe drying they are able to use almost the whole of their stored water. The low rates of transpiration involve low rates of photosynthesis, the stomata being closed. This adversely

affects growth. The cacti are, therefore, slowgrowing plants. The stomata are usually open during the night and are closed by day. This unusual feature is associated with their peculiar method of metabolism. During the night these plants produce acids in the process of respiration. The acids are further decomposed to produce carbon dioxide only in sunlight. The stomata being then closed, the carbon dioxide thus produced does not leave the plant, but is at once used up in the process of photosynthesis. Another effect of slow expenditure of water and low rates of photosynthesis is that these plants possess low osmotic pressure.

In the second category of succulents are plants like the *Aloe* and *Agave* in which the leaves become succulent and the stem is reduced. The leaves are vertically erect and their epidermis shows special features. The cellulose layer of the outer epidermal wall is very thick with heavy cutinisation and a thick cuticle. In addition, a waxy covering is developed as in *Agave*. Inside the epidermis are several rows of chlorenchyma with abundant chloroplasts followed by a large water storage tissue in the pulpy interior. The stomata are sunken. The highly developed cuticle greatly reduces water loss when the stomata are closed.

The succulents are drought resistant plants rather than those that endure drought. They illustrate clearly the principle that unrelated plants, under similar environmental conditions develop striking similarities in external form. Thus, plants belonging

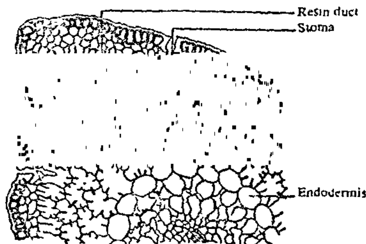


Fig. 3.1. T.S leaf of *Pinus*. Note the thick cuticle and the hypodermis, sunken stomata and the mesophyll cells with infolded walls

to the Euphorbiaceae show such marked resemblance to some of the cacti that in the absence of the flower they might be considered close relatives.

The most interesting types of xerophytes are the desert plants or true xerophytes, which include perennial herbs as well as woody shrubs and small trees. The leaves may be thin and rigid (sclerophyllous) due to the great development of sclerenchyma or else they are thick and leathery. These plants are usually shrubs with small aerial parts and an extensive root system which may grow deep and reach the water table or spread profusely to command a large area of the soil for water absorption. The root hairs are abundant, often extending far back from the root tip. Their transpiring surfaces show many peculiarities. Among these are the shiny glazed surface of the leaves and stem from which light is reflected (Oleander). The leaves and stems are clothed with a dense growth of hairs (Calotropis). The cuticle es the epidermis is extremely cutinised making the leaves leathery (Banyan). A thick hypodermis is often developed internal to leaf epidermis (*Calotropis procera*). These characters tend to greatly reduce or completely prevent cuticular transpiration. The stomata are sunken in depressions or contained in special cavities beneath the epidermis (Figs. 3.1 and 3.2), thus protected from wind action. They may further be protected by hairs, or heavy cutinisation or both. The mesophyll is differentiated into palisade tissue and spongy parenchyma. Mechanical tissue is prominent in the leaves. This occurs in the form of sclerenchyma fibres in or around the bundles and a hypodermis of lignified fibres or cutinised cells immediately beneath the epidermis. These help to keep the leaf in a rigid condition even when wilted. Thus, wilted stems and leaves of xerophytes do not droop like those of mesophytes, which have lost their turgor. The palisade is compactly arranged, the size of the cells is smaller than in similar plants grown in moist habitats, and the intercellular spaces are small. A marked reduction in the size of cells including the guard cells is a general feature of the anatomy of xerophytes. As a consequence, the leaves remain small, the stomata are close to one another, and more numerous per unit area and the veins form a denser network than in mesophytes. Plants on the whole remain small. Accompanying the decrease in the size of cells is a distinct increase in the thickness of walls. This is

due to the conversion of polysaccharides into their anhydrides or wall materials (cellulose, etc.) as a result of reduced water supply in the cells. As a consequence, a general induration of plant structures takes place, which is a characteristic feature of desert plants. Lignification and annual rings are prominent features of xerophytes. Conducting elements are numerous, longer and larger than in mesophytes. Bast fibres and sclerenchyma reach their maximum development in xerophytes. Desiccation

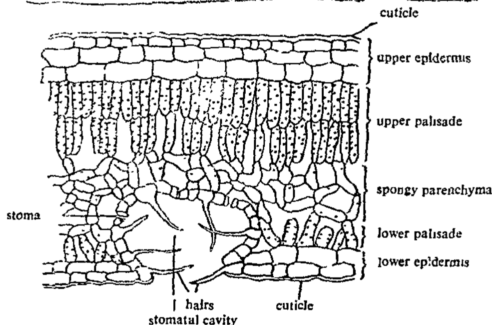


Fig. 3.2. T.S. leaf of oleander. Note the thick cuticle, many layered upper and lower epidermis, compact palisade, and the depression in the lower epidermis containing a group of stomata protected by hairs. (Drawn by T.S. Bakshi)

promotes the development of cork. The thickness of the bark increases with increase in the drought conditions. The leaves of desert plants have a dull-greyish colour in constrast to the bright green of mesophytes and hydrophytes. This is due to the thick cuticle, or because the chlorenchyma is more deeply situated or because of the small number and pale colour of the chloroplasts. Because of utilisation of carbohydrates in the formation of cell wall material, growth is slow. Plants of xeric habitats are, therefore, commonly dwarf. Intense light and extreme desiccation also promote the development of spines on the stem and leaves. In many xerophytic grasses the leaves role up during times of water deficiency so that the upper surface which bears the stomata

becomes the inner surface of the rolled leaf and the stomata are protected from wind action. In the *Psamma* grass the upper surface consists of a number of ridges and grooves with stomata situated near the base of the sides (Figs. 3.3, 3.4). The cells at the base of the grooves are large and thin-walled (hinge cells) and the tissues round the grooves and on the sides of the ridges are chlorenchymatous The rest of the leaf tissue is mostly mechanical. In times of water scarcity, the hinge cells lose water more rapidly than the other cells which are strongly cuticularised. The result is that the two

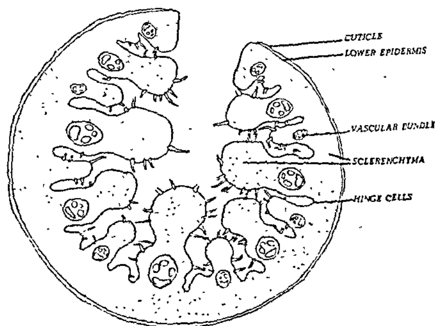


Fig. 3.3. T.S. leaf of *Psamma*

sides of the grooves are drawn together and the leaf rolls up, thus protecting the stomata. In this process the mechanical tissue effectively prevents the collapse of the leaf. The lower epidermis becomes the outer surface. When water is available and the atmospheric conditions not so severe, the whole mechanism is reversed and the leaf unrolls. In legumes, the same result is obtained by the folding of leaves or leaflets in pairs.

For a long time it was believed that the xerophytes were characterised by low rates of transpiration and the various structural peculiarities described above acted as checks on transpiration. This view has been shown to be erroneous by Professor Maximov. His



Plate 6. Different forms of Cacti (succulent xerophytes)

(Photo by Prof. P.C. Joshi)

Text reference on page 52]

[To face page 56



Plate 7. *Opuntia*, a typical succulent xerophyte
(*Photo by S Paul, Simla*)

Text reference on page 52]



Plate 8. *Euphorbia sp.*, a typical xerophyte

(*Photograph by Prof. P.C. Joshi*)

Text reference on page 52]



Plate 9. A Rakh at Chhanga Manga (West Pakistan) Showing *Capparis aphylla*, a leafless xerophyte, in the foreground
(Photograph by Prof. P.C. Joshi)

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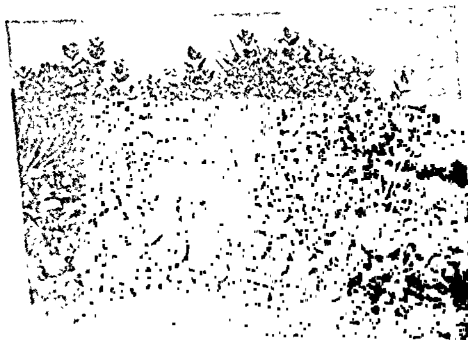


Plate 10 *Calotropis procera*, a typical xerophyte

(Photograph by Prof. B. N. Sood

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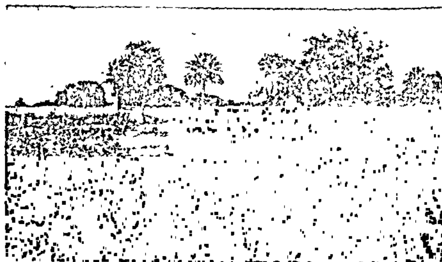


Plate 11 *Argemone mexicana*, an annual xerophyte

(*Photograph by Prof B.N. Sood*)

Text reference on page 61]



Plate 12. *Vanda roxburghii*, an epiphytic orchid, growing in eastern Bihar. Note the dangling thread-like epiphytic roots and thick leathery leaves.

(*Photo by Prof. A.B. Saran*)

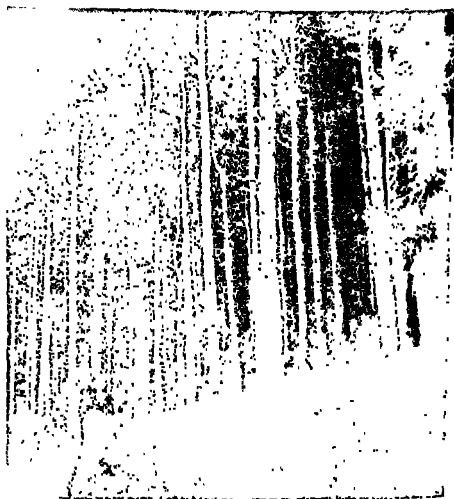


Plate 14. Forest of *Cryptomeria Japonica* at Darjeeling 7,000 ft above sea level

(*Photograph by Prof. B N. Sood*)

Text reference on page 101]

[*To face page 57*

work, which is supported by a large amount of experimental evidence, goes to
true xerophyte
normal condit
that of mesophytes. Xerophytes possess more stomata per unit area of leaf surface, though the total number of stomata on a xerophytic leaf is less than on the leaf of a mesophyte because of the comparatively small size of the leaves of xerophytes. The leaves may be smaller than those of the mesophytes but the stomata are more numerous per unit leaf surface. More xeric the conditions, greater

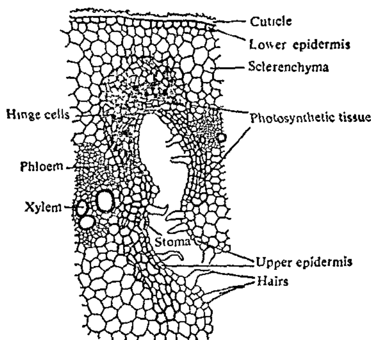


Fig. 3.4. A part of figure 3.3 highly magnified, showing detailed structure of a portion of *Psamma* leaf between two ridges

is the stomatal frequency. Thus, in the same plant, the higher leaves (and they are farther from the source of water) have a larger number of stomata per unit area than the lower ones. In dicotyledons, the stomatal frequency increases from the base to the apex and from the midrib to the periphery. In other words, parts farthest removed from the water supply and having the least quantity of water have the largest number of stomata per unit area. In the forest flora, the greatest frequency of stomata was found in the tree layer, which is exposed to greatest desiccation, and the least in the

brings about closing of the stomata and wilting of the plant. It is at this time that the xeromorphic structures of the plant are useful. These cut down the cuticular transpiration to very low limits so that in the wilted condition the water loss from the plant is almost nil. Under such conditions the plant remains in the wilted state but still alive. Due to the closure of the stomata photosynthesis and other metabolic activities are also at a low ebb, but the plant is able to withstand all this. In the mesophytes, even after the wilting of the leaves, cuticular transpiration continues, ultimately leading to the death of the plant. Xerophytes are characterised by reducing their water loss to a minimum in times of water scarcity and by their capacity to survive long periods of drought and dehydration of their tissues without injury or with only slight injury. Thus, the chief peculiarity of xerophytes seems to be the increased power of resistance of the protoplasm to injury during wilting. The extensive resistance to wilting is in some way related to the high osmotic pressure of xerophytes, which again is the result of high rates of transpiration. The xerophytes do not wilt so rapidly as the mesophytes do. While mesophytes wilt with a small reduction of their water content (even 1 to 2%), xerophytes may lose 8 to 25% or more of their water before they wilt. With the return of water conditions more favourable to growth, a xerophyte will recover and start its activities anew. In the deserts also, relatively short but comparatively favourable periods occur when the atmosphere is cool and humid. The desert plants are characterised by their ability to become active during such periods. This happens when there is a little rain and during the short periods that follow when water is available for plant growth. They are especially active in the morning because the plants are then sufficiently saturated with water that has accumulated in the tissues during night when the stomata were closed. Xerophytes are drought-resistant plants rather than plants which are benefitted by xeric conditions. Under favourable water conditions, their growth and yield are greatly increased.

From the foregoing discussion it should be clear that the explanation of drought resistance in xerophytes should be sought not in xeromorphic structures but in such physiological properties of the protoplasm as high osmotic pressure, water binding properties of the hydrophilic colloids of the living protoplasm, and the ability of the protoplasm to continue its vital activities and resist

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irreversible coagulation even under conditions of extreme dehydration.

The xeromorphic adaptations described above are not met with in all true (non-succulent) xerophytes. Many desert shrubs have thin leaves, and show a high rate of transpiration when water is available. Their root systems are extensive, penetrate deep into the soil and are densely clothed with root hairs. During periods of drought, their leaves dry up, become brown and shrivelled up, and fall off. The leaves may reappear in a few days following even moderate precipitation. This phenomenon may be repeated several times in a year. In other deciduous trees and shrubs, an annual leaf fall occurs as an adaptation to periodical drought.

In many species the leaves are greatly reduced or wanting or reduced to scales or spines (*Ruscus*, *Asparagus*, *Casuarina equisetifolia*, *Capparis aphylla*, *Tamarix dioica*, *T. articulata*) ; in some they are few and present only for a short period ; and in still others they are narrow and needlelike (*Pinus*).

In many xerophytic plants the stem is very much reduced hardly coming above the surface of the soil, with internodes that are little or not at all developed. The leaves, which are radical appear to arise directly from the base of the root and either lie flat on the soil surface in the form of a rosette or else form a cluster of semi-erect radiating leaves that are stiff or fleshy as in *Agave* and *Yucca*.

A list of common xerophytes is given below.

1. *Acacia arabica* (**Babul or Kikar**). A tree, leaves compound bipinnate, pinnules small, oval, stipulate, stipules modified into spines which serve as organs of defence and reduce transpiration. Grows wild in arid regions.

2. *Acacia modesta* (**Phulai**). A small tree, leaves bipinnate pinnules reduced, stipulate, stipules modified into spines to serve as defence organs. Grows wild in arid regions.

3. *Agave americana* (**Jangli Keora**). It grows wild in arid regions. A xerophyte with rhizome and massive rosette of spiny leaves which are thick, fleshy and coated with wax.

4. *Aloe vera* (**Kanwar gandal**). Leaves long, cuspidate succulent and store water. Grows wild or cultivated for medicinal purpose.

5. *Alhagi maurourm* (**Unth chara or Jawan**). A low thorny

xerophytic shrub ; shoots modified into thorns to cut down transpiration. Thorns bear red flowers. Wild in dry sandy soil ; roots very long and grow very deep to absorb water.

6. *Argemone mexicana* (**Jangli Post**). Very common in fields and waste places. Leaves and stem covered with pointed bristles, latex yellow. Flowers large and yellow, usually during March-April.

7. *Calotropis procera* (**Ak**). Wild shrub, common in arid and waste places, with thick leathery leaves. Stem and leaves mealy ; latex viscid and milky ; flowers scented.

8. *Capparis aphylla* (**Karir, Dela**). A much branched glabrous shrub ; twigs smooth, green with nearly straight paired spines ; leaves small, on young shoots only and fall off very early.

9. *Carthamus oxycantha* (**Pohli**). A troublesome weed in the wheat fields, extremely spiny all over : flowers yellow. The plant gets uprooted on drying and rolls in big masses before the wind, scattering the seeds in the fields which again grow in the next season.

10. *Echinops echinatus*. Wild in arid places ; extremely spiny all over, heads prominent with many stout spines ; florets bluish-white.

11. *Euphorbia prostrata* (**Dodak**). A very common weed, forming rosettes round its root stock ; leaves small, sub-sessile, elliptic, latex white and viscid.

12. *Euphorbia royleana* (**Danda thor**). Wild or cultivated as a hedge plant ; cactus-like shrub with latex ; leaves succulent, appearing in spring and rainy season but soon fall off, stem angular, bearing spines in pairs : latex white and viscid.

13. *Opuntia dillenii* (**Chittar thor**). Wild on dry soil, employed as a hedge. Stem modified into phylloclade, jointed, succulent, storing water ; leaves reduced to spines forming clusters or areoles.

14. *Prosopis spicigera* (**Jand**). Prickly tree or shrub, in arid regions : leaves compound, bipinnate, used as fuel.

15. *Solanum xanthocarpum* (**Kandiali**). Wild in dry places, with yellow prickles all over ; flowers bluish purple ; fruit a yellow berry, or white streaked with green, supposed to have medicinal properties.

16. *Salsola foetida* (**Lana**). Wild, densely branched hairy under-shrub common in saline soils, leaves crowded, minute, fleshy and store water. Sajji is prepared from the plant as it abounds in

alkali salts.

17. *Suaeda fruticosa* (**Saloonak butl**). Wild undershrub, common in saline soils, often gregarious ; leaves subsessile, succulent, green purplish, Sajji is obtained from this plant also.

18. *Tribulus terrestris* (**Bhakhra**). Prostrate herb with very minute mealy leaves ; fruit spiny.

19. *Zizyphus jujuba* (**Ber**). A moderate-sized tree ; leaves, small, mealy, stipules modified into spines.

20. *Zizyphus nummularia* (**Malah**). A thorny tomentose bush, common in dry places ; leaves coriaceous with hairy or bloomy coating, stipules modified into spines.

Study the following xerophytes also if available and collect them for your album :—

(*i*) *Tamarix dioica* (**Pilchhi**)
(*ii*) *Butea frondosa* (**Dhak**)
(*iii*) *Tamarix articulata* (**Farash**)
(*iv*) *Salvadora oleoides* (**Pilu**)
(*v*) *Saccharum moonja* (**Sarkanda**)
(*vi*) *Nerium odorum* (**Kaner**).

HALOPHYTES

Xerophytes are the characteristic plants of the deserts where xerism is due to hot and dry climate. But xerophytes are by no means confined only to the deserts. They are met with in a great variety of habitats where the cause of xerism may be other than the arid climate. Thus, plants that grow on rocks, sand or gravel are xerophytes because the substratum is physically dry. Similarly, plants growing on seashore where the soil is periodically flooded with salt-laden sea-water show pronounced xerophytic characters. On the seashore there is abundant water in the soil and the air is humid but the plants are faced with great difficulty in the matter of water absorption on acco [illegible] of salts in the soil. Such soils are [illegible] habitats are called **halophyt**[illegible] are inhabited for the most part by algae which do not show xeric characters. The reason is that by virtue of their being submerged in water they are protected from transpiration.

[illegible] drought the halophytes show [illegible] The halophytes of the temperate [illegible] tropical and subtropical regions

the seashore is occupied by a dense woodland of trees called mangrove forests. The mangrove trees show marked anatomical and physiological peculiarities. Their leaves are thick and succulent on account of water storage tissue, the palisade tissue is prominently developed, and the epidermis is heavily cutinised. The succulence of the leaves is accompanied by very high osmotic pressure. This combination of xeric characters is a remarkable feature of the halophytes as a group. Many mangrove trees develop numerous prop roots which hang down from the stem branches as in *Rhizophora.* These go down through the water and finally reach the soil below. Frequently special negatively geotropic roots arise from the normal subterranean roots. These grow up straight into the air above the surface of mud like so many knees, as in *Sonneratia.*

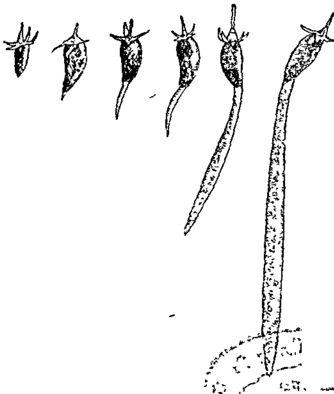


Fig. 3.5. Viviparous germination of seeds in mangrove plants.

These pneumatophores, as they are called, possess lenticels and a [illegible] ces through [illegible] halophytes is

vivipary, by which is meant the germination of the seed while it is still attached to the parent tree. In *Rhizophora*, germination of the seed within the fruit may result in the elongation of the hypocotyl to a length of 10-15 inches, pushing out the radicle before it falls down vertically like a dart (Fig. 3.5). If it falls on mud, it gets stuck up and soon develops lateral roots. If it falls in water, it keeps afloat vertically until it reaches shallow water where it may get fixed up as above.

Mangrove plants occur on the eastern and the western coast of India and the Gangetic delta in Bengal. A description of the mangrove vegetation will be found in chapter 5.

We have already spoken of the alkali soils (page 33). Besides being physiologically dry, these are often also physically dry and therefore unfit for ordinary and crop plants. Only especially salt tolerant species can grow in such habitats. These plants are strikingly xeric. They possess very high osmotic pressure combined [illegible]

(*Salsola foetida*) or fleshy (*Suaeda fruitcosa*). The leaves of tamarix have glands that secrete chalk which can absorb moisture from the air.

EPIPHYTES

Epiphytes are plants that grow perched on other plants. The epiphytes are quite distinct from the parasitic plants on the one hand and from the climbers and twiners on the other. They differ from the former in the fact that they contain chlorophyll and are autotrophic plants which have no food relation with the plants on which they grow. From the latter group they are distinguished by the fact that they are not connected with the soil. They absorb water from the rain or dew drops that fall on them or from the moisture contained in the air.

Epiphytes grow abundantly in the dense tropical rain forests. They are also met with in the temperate forests and are common in the eastern and western Himalayas. It appears that the epiphytic habit has been developed as a response to the light factor. The absence of epiphytes from the open vegetation and their abudance

in the forests where the dense growth of trees casts a deep shade on the forest floor lend support to this view.

The plants that constitute the epiphytic flora range from the thallophyta to the flowering plants. Among the epiphytic lower plants of the Himalayas are lichens, mosses, and ferns like *Drymoglossum* and *Asplenium nidus*. Among the flowering plants, the most conspicuous epiphytes are the orchids. The Himalayan epiphytes of this class are given below

1. Family Orchidaceae	*Vanda, Dendrobium* and *Bulbophyllum.*
2. Family Araceae	*Pothos scandens, Scindapsus* and *Rhaphidophora.*
3 Family Moraceae	*Ficus ramentacea.*
4 Family Asclepiadaceae	*Dischidia*, an epiphytic pitcher plant of the Sunderbans.

The epiphytic higher plants are well represented in the tropical rain forests. Besides the epiphytic orchids like *Vanilla, Taeniophyllum* and *Polyrrhiza,* there are many plants of the family Bromeliaceae. This family consists mainly of tropical epiphytes. *Tillandsia usneoides* is a common example.

The epiphytes have developed many adaptations to meet the special situation in which they live. These plants grow on the horizontal branches or in the forks of the tree branches. They must be held firmly to the supporting tree in their early stages of growth to prevent their being blown away by wind or washed down by heavy r[illegible] of clasping roots as in F[illegible] These roots are irritable a[illegible] trees. The second and more important problem for these plants is that of water supply. Th[illegible] only source of water is [illegible] rain, dew or moistu[illegible] water absorption is of a doubtful nature and water may not be always available to the plants. Moreover, the rain water readily flows away and does not accumulate. The epiphytes are, therefore, xerophytic plants which have developed many peculiar adaptations for absorbing and storing water and economising in its use.

The adaptations of epiphytes for absorbing water from rain

and dew drops are many and varied. Many epiphytic orchids and aroids develop lon[illegible] the air. These roots [illegible] which develops on [illegible] cells are dead and have holes in t[illegible] water like a sponge from rain an[illegible] the roots. The velamen cells, being hygroscopic, can also absorb moisture from the humid air. In many cases dust particles collect in the tree-forks and some humus is formed there from the tree bark or from the dried and fallen leaves of the epiphyte, forming a little soil. After rains this soil becomes soaked with water. The roots of many epiphytes can absorb water and minerals from this wet soil. In others, the roots spread over the bark of the supporting tree and absorb rain water that may be lying in the crevices of the bark. In some epiphytes, for example *Tillandsia usneoides* (Araceae), hygroscopic epidermal hairs or scales are developed. These readily absorb water. In *Dischidia* (Asclepiadeceae), leaves are modified into pitcher-like structures in which rain water collects. Adventitious roots then absorb this water. In many species of *Tillandsia*, leaves are shaped like gutters where water can collect.

The epiphytes possess many peculiarities for cutting down water loss by transpiration during dry weather. Their leaves are thick and succulent and store water as in *Vanilla*. In *Ficus ramentacea*, water is stored in the many-layered epidermis of the thick leaves. The cuticle is thick and the stomata are sunken. In others the leaves are reduced, or altogether absent as in *Taeniophyllum* and *polyrrhiza*. These plants have no green leaves and the photosynthetic function is performed by the green stem or by the roots which turn green. Many of the epiphytes shed their leaves in the dry weather and pass this period as pseudobulbs which consist of a few internodes that are succulent and store water. Above all, the epiphytes are capable of enduring desiccation. The xerophytic characters of the epiphytes, described above, enable them to cope successfully with the conditions of their habitat.

BOG PLANTS

Another [illegible] ...ically dry habitat is the bog. There is abundanc[illegible] ...es the soil water-logged. T[illegible] bacteria thrive.

This leads to an accumulation of carbon dioxide and organic acids in the soil. Some of the products of bacterial metabolism are toxic to the roots. The water also becomes acidic. Under these conditions, absorption of water by the roots is very difficult. The plants, therefore, show marked xeric characters. A special feature of the bog plants is the formation of large intercellular spaces and a system of well-developed air cavities in their roots. These communicate with similar cavities in the stem and leaf-stalks. Oxygen formed during photosynthesis is forced down towards the roots and there it is used for respiration.

ALPINE PLANTS

Another class of xerophytes are the plants that grow on mountain tops above the timber line (above 11,000 or 12,000 ft.). In these alpine regions, scanty precipitation, strong dry winds, intense insolation and severe cold combine to create the most xeric conditions.

As the conditions are not favourable for growth, the plants remain dwarf. Plant species that form tall trees a few hundred feet down the mountain become shrubby at 11,000 or 12,000 ft. altitude forming the characteristic "elfin timber". Above this grow only grasses and herbaceous flowering plants forming alpine meadows in open spaces. The herbs bear brilliantly coloured flowers in summer and winter. The plants are mostly perennial, since the growing season is too short for the completion of vegetative and reproductive growth. Vegetative reproduction is common.

The plants are characterised by deep rooting, leaf reduction, succulence, waxy surface or hairy covering Many of them have a rosette habit. This protects them from the strong winds. These plants can withstand very low temperatures ; they remain buried under the snow for the greater part of the year, but become active when the snow melts. They are capable of carrying on photosynthesis at a comparatively low temperature. Their tissues contain a high percentage of sugar which accounts for their high osmotic pressure. This gives them strong water-absorbing power and increases their hardiness to the low temperatures that prevail in alpine regions. All these are xerophytic characters. Some common Indian alpine herbs are species of *Potentilla, Saxifraga, Primula, Corydalis, Delphinium* and *Anemone*. Most of the species are endemic, *i.e.*, they are confined to one definite locality, either

one mountain or group of mountains ; they are not found in the valleys below.

An important feature of the alpine vegetation is the group of cushion plants. The plants are dwarf and the stem branches, clothed with small overlapping leaves, are so dense and compactly arranged as to form more or less solid mats or cushions. The cushion habit gives them protection against the winds. Examples of cushion plants are *Arenaria, Cragna* and *Androsace.*

MESOPHYTES

These are plants of habitats which are neither extremely dry nor very wet. The soil solutions are dilute and the soil contains adequate oxygen supply for the roots. Many of our cultivated crop and garden plants and the ground flora of the deciduous and evergreen forests belong to this The mesophytes are inter-
mediate between xerophytes a
characteristics. They are often
phytes. There is plenty of water in the soil and the roots are very prominently developed with extensive branching and abundant root hairs. The volume of roots often equals or exceeds that of aerial parts. The foliage is very richly developed and the leaves are large and thin. The epidermis is thin and the chloroplasts are abundant and the leaves appear dark-green as compared with the pale-green leaves of the xerophytes. Stomata occur usually on both surfaces except in the woody trees where they are confined to the lower surfaces only. There are no devices for protecting the plant against cuticular transpiration, the cutinisation of epidermal walls being very moderate. In fact, in many mesophytes the cuticular transpiration is as rapid as stomatal transpiration. These plants readily wilt even under conditions of slight water deficit. In fact, many mesophytes show temporary wilting during the noon hours of summer. If the water deficit is not readily made up, temporary wilting may give place to permanent wilting from which the plants may not recover unless quickly watered. Even then the recovery is very slow. Unlike the xerophytes, these plants do not possess any pronounced resistance to wilting. Their osmotic pressure is also low as compared to the xerophytes.

HYDROPHYTES

These are plants which grow wholly or partly submerged in

water. Water conditions being uniform, there are fewer adaptations in aquatic plants than in xerophytes which grow in most varied conditions. The plants readily fall into two categories viz., submerged and floating. The latter may be free-floating or rooted in the mud with only leaves floating on the water surface. The rooted plants are better adapted as they easily obtain mineral supply from the mud at the bottom of water. As already emphasised, the two factors which have the greatest influence on plant life are the supply of water and the regulation of transpiration. In the case of hydrophytes, water is easily accessible and in the case of submerged plants transpiration is out of question. The absorbing and conducting tissues are, therefore, reduced to a minimum. The roots are poorly or not at all branched. In some cases they are altogether absent (*Wolffia*, *Ceratophyllum*, *Salvinia*, *Utricularia*).

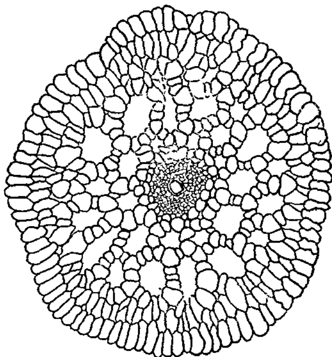


Fig. 3 6. T.S. stem of *Hydrilla*, showing aerenchyma and the central xylem cavity surrounded by phloem

In others they soon cease to grow and do not branch (*Azolla*, *Lemna*) and often have root pockets that fit over the ends of roots, but have no root cap. The function of root pockets is not understood. The roots are mostly devoid of root hairs (*Lemna*

minor, *Nymphaea*). Even the older roots are not cutinised suberised. The xylem, being less in demand, is poorly-develop and reduced, its place being often taken by a central cav surrounded by phloem which remains unaffected as in *Hydri* *Potamogeton* and *Vallisneria* (Figs. 3.6, 3.7, 3.8). In the submerg leaves, the stomata are altogether lacking and, when prese are functionless, indicating the land ancestory of the plants. T floating leaves bear stomata on the upper surface only. The epid mis is thin and cuticle is almost wanting. But their upper surface h a waxy coating that prevents wetting and clogging of stomata. the submerged plants transpiration in the strict sense is excluded b excretion of water takes place by guttation through water pores hydathodes. T and the plants

On account is not needed and is, therefore, reduced or undeveloped. *Lignifica*tion occurs too little or not at all. The plants are, therefore, so

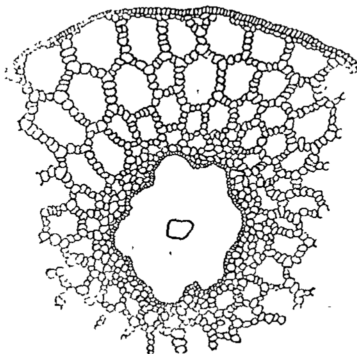


Fig 3.7. T.S stem of *Potamogeton*, showing prominent *aerenchyma*. The axial cylinder is not shown but the position of the small central xylem cavity is indicated

and tender. Among submerged plants there are no woody plants. On account of non-development of mechanical tissue near the periphery, the chlorenchymatous cortex is much larger. This increases photosynthetic activity. The stems and leaves are sometimes covered with a slimy mucilage to guard against the rotting effect of water.

The two other important external factors which influence the submerged water plants are poor supply of air and weak light. These plants, like others, need oxygen for respiration and carbon dioxide for photosynthesis. The hydrophytes have solved this [illegible] a system of air spaces or [illegible] n the submerged parts so that all the tissues can obtain enough oxygen for respiration by internal circulation (Figs. 3.6 to 3.9).

Light intensity weakens with the depth of water, as some of it is absorbed by the solid particles suspended in water. Submerged plants, therefore, become weak, etiolated and thin and their assimilatory tissues show little differentiation. The entire mesophyll is chlorenchymatous and the chloroplasts are present

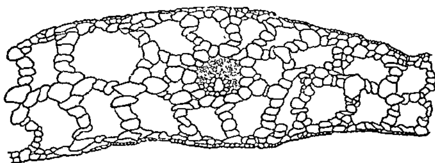


Fig 3.8. T.S. leaf of *Vallisneria* showing aerenchyma and the xylem cavity

abundantly even in the epidermis. Leaves are very much dissected, often ribbon-like, thin and linear, being 1-2 or 3-cell thick. This greatly increases the surface for absorbing carbon dioxide from water. Thin leaves present an increased surface, in proportion to tissues involved, for the absorption of diffused light also. The plastids are large and mobile. In the floating leaves, palisade is well-developed but is far exceeded by the spongy tissue which has large air chambers. Isolated sclereids (thick-walled sclerenchymatous cells) are also present beneath the upper epidermis and furnish mechanical support.

Floating plants that are rooted have long horizontal rhizomes, or have rootstocks or tubers and form large communities. The leaves have very much elongated petioles.

On account of uniform and favourable conditions, vegetative propagation is very common. *Elodea* reproduces by fragmentation, and *Eichhornia* by runners.

A list of common aquatic plants is given below :

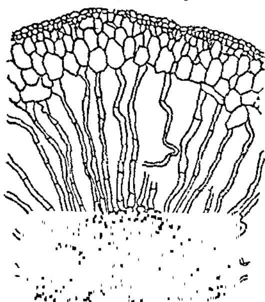


Fig. 3.9. T.S. root of *Eichhornia*, showing aerenchyma

A. Submerged water plants.

1. *Hydrilla verticellata.*
2. *Vallisneria spiralis.*
3. *Potamogeton crispus.*
4. *P. pectinatus.*
5. *Zannichelia palustris.*
6. *Trapa bispinosa.*
7. *Utricularia.*
8. *Ceratophyllum demursum.*

B. Free-floating plants.

1. *Lemna polyrrhiza* and *L. paucicaustata* (Duckweeds).
2. *Wolffia arrhiza* (Duckweed).
3. *Eichhornia crassipes* (water hyacinth).
4. *Salvinia natans* (water fern)
5. *Azolla imbricata* (water fern).
6. *Pistia stratiotes.*

C. **Floating plants rooted in the mud.**

1. *Nymphaea lotus* (water-lily).
2. *Nelumbium speciosum* (Lotus).
3. *Victoria regia* (water-lily).
4. *Marsilia quadrifolia* (water fern).

An allied category of plants is that of amphibious or emersed plants. These are dealt with in the next section.

AMPHIBIOUS OR EMERSED PLANTS

Plants of this group inhabit shallow waters. Their roots, parts of stem and often portion of leaves are under water but a portion and often most of the shoot is aerial. These plants are thus adapted to live partly in water and partly in air. The two partial habitats have a marked effect on the plants. Common examples are *Ranunculus aquatilis* (water crow-foot), *Sagittaria* (arrow head) and *Alisma plantago* (water plantain).

Swamp plants come in this category. A swamp is a marshy land, where the water table is just near the soil surface. Growing on the edge of water, these plants are subject to periodic inundations. At times, the soil is actually under water and, at others, the water table recedes below the surface of the soil which becomes saturated to a considerable depth. Plants growing under such conditions readily adjust themselves to the changing conditions and may live as mesophytes or partly submerged. Characteristic plants of such habitats are the cattails (*Typha*), the reed (*Phragmites*), and the bulrush (*Scirpus*).

The amphibious plants have well developed and rapidly spreading rhizomes or rootstocks fixed in the mud by adventitious roots. The development of roots is determined by the increase in water and decrease in aeration. As the plants grow in two partial habitats, they show a mixture of mesophytic and hydrophytic characters and also some xeric characters due to lack of aeration in the water-logged soils. Like the mesophytes, the plants have a well-developed conducting and mechanical tissue and like the hydrophytes they have an abundant storage parenchyma and a system of large air chambers for internal aeration of the submerged parts. The endodermis is thick and guards against water loss in times of drought, a xerophytic character. The presence of conducting and mechanical tissue enables the plants to grow erect. Either the green stem or leaves grow vertically straight for

photosynthesis. These characters are well illustrated in *Typha.*

The leaves of amphibious plants show heterophylly. Th submerged leaves are thin, often very much dissected, have n cuticle or stomata or else only functionless stomata. These ar adaptations for the absorption of carbon dioxide from th water. The mesophyll is all spongy tissue with large air chamber The aerial leaves are usually large and entire or only slightly lobed showing a tendency to increase the exposed surface. These feature are illustrated in *Ranunculus aquatilis* and *Sagittaria sagittifolia* Compared with the mesophytes, the aerial leaves have a thin cuticl and are without protective hairs. Stomata are present, being mor numerous on the upper than on the lower epidermis. The meso phyll is differentiated but the palisade is very thin, consisting onl of one or two rows. The spongy tissue is much in excess wit prominent aerenchyma. The conducting tissue is more efficient thar in true hydrophytes.

Ecological notes on some common hydrophytes.

Ranunculus aquatilis (water crow-foot). It is an amphibious

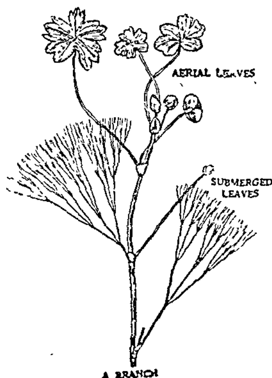


Fig. 3.10. *Ranunculus aquatilis*

aquatic herb. Leaves are dimorphic and show heterophylly. The submerged part of the stem bears deeply cleft hair-like leaves, while the aerial leaves are three-lobed, and variously cut. Flower is large, white and conspicuous, borne singly on axillary flower-stalks (Fig. 3.10).

Sagittaria sagittifolia. It is an aquatic herb growing partly in shallow and partly in deep water. The rhizome is thick and stoloniferous, stolons often ending in tubers. Leaves are dimorphic and heterophyllous. Leaves in deep water are strap-shaped, lanceolate or elliptic, while those in shallow water are erect with hastate or sagittate lamina. Petiole is long, trigonous and spongy. Flowers unisexual arranged in whorls on long scapes (Fig. 3.11).

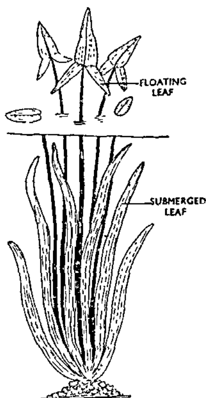


Fig. 3.11. *Sagittaria sagittifolia*

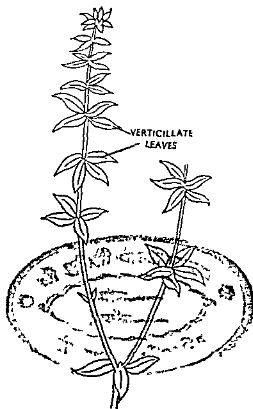


Fig. 3.12. *Hydrilla verticellata*

Hydrilla verticellata. It is a common submerged water plant in the shallow water of fresh-water ponds, lakes, tanks and streams. It is attached below to the substratum by fibrous adventitious roots. The stem is weak, soft and slender divided into nodes and internodes. It is freely branched. At the upper nodes

the leaves are arranged in whorls of 3 to 4 but on the lower nodes they are opposite. Leaves are green, thin, sessile, linear or lanceolate in outline, unicostate and entire. It is commonly used in aquaria as it is a good oxygenator and releases oxygen for the fish and other aquatic animals. The entire plant is coated with mucilage which protects it against the rotting effect of water. Reproduction is both vegetative and by seeds. Flowers are minute and dioecious ; Male solitary, pedicellate, in mucronate spathe, female sessile, 1-2 in a tubular spathe (Fig. 3.12).

Vallisneria spiralis (Eel grass or Tape grass). It is a submerged aquatic plant, commonly found attached to the substratum in shallow fresh-water ponds, lakes and tanks by fibrous, adventitious roots. It is tufted, either stemless or the stem is reduced, bearing a number of green long ribbon-like radical leaves which are 5-nerved, entire and serrulated at the tip. Male flowers many, in shortly stalked spathe; female flowers solitary within 2-3-toothed spathe on a spiral stalk.

Ceratophyllum demursum (Fig. 3.13). It is a submerged aquatic plant, which floats freely and more or less erect in fresh-water ponds and streams. It lacks roots and is, therefore, not attached

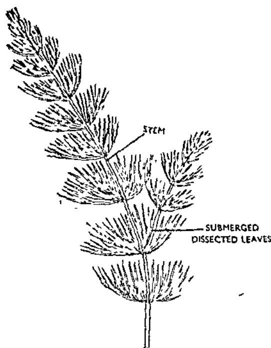


Fig. 3.13. *Ceratophyllum demursum*

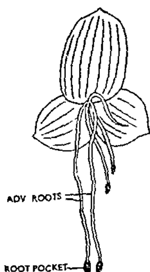


Fig. 3.14. *Lemna polyrrhiza*

to the substratum. The stem is long, slender and branched. Branches arise singly at the nodes. Leaves are rigid and olive-green in colour. They arise in whorls of 6-10. Each leaf is dissected dichotomously, and the segments grow into long, slender filiform structures which are serrate on the outer edge. The leaves are more over-crowded towards the apex than towards the base. The flowers are solitary and axillary.

Lemna polyrrhiza (Duck-weed). It is a small, free-floating, fresh-water herb, commonly found in tufts on the surface of still waters of ponds and lakes. The plant shows no differentiation into distinct stem and leaves. The plant body is reduced to an oblong, flat, globose thallus, consisting of 2-5 green fronds, bearing a number of ventrally attached adventitious root. The root is devoid of root hairs and vascular tissues, but bears a prominent root-cap. The fronds are thickly cutinised on the dorsal surface which protects them against overwetting. Flowers are minute and unisexual.

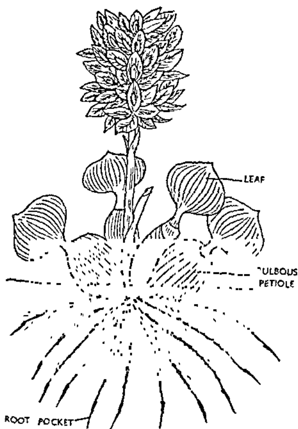


Fig. 3.15. *Eichhornia crassipes*

Plants are monoecious. Male flowers are solitary or in pairs, while the female flowers are solitary. Internally, the thallus consists of spongy parenchymatous cells having air spaces. (Fig. 3.14).

Eichhornia crassipes (Water-hyacinth). It is a floating aquatic herb, very common in village ponds and tanks. The stem is short and bears a large tuft of pinkish adventitious roots ventrally, immersed in the water and long-petiolated, green, radical leaves dorsally, emerging out of water. The lamina is thick, fleshy and ovate-rhomboid in outline, covered with a glossy water-proof cuticle to prevent over-wetting. The petiole is swollen into a bladder-like structure which is highly spongy and enclosing copious aerenchyma keeps the plant floating on the surface of water (Fig. 3.15).

Pistia stratioites (Water cabbage). This is a floating aquatic herb, common in ponds. Stem is stoloniferous, bearing rosettes of

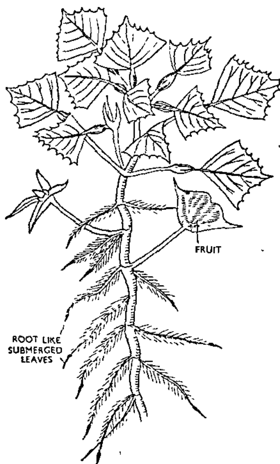


Fig. 3.16. *Trapa bispinosa*

roundish, spathulate or obcordate cuneate leaves, the outer of which lie on the water while the inner stand erect. The leaves in the rosette remain closed at night, but open into a horizontal position by day. Stolons grow out from the leaf axils which give rise to new vegetative plants. Cluster of adventitious roots rise ventrally at each node. The inflorescence is small and monoecious consisting of a whorl of male flowers above and female flowers below.

Trapa bispinosa (Water chestnut). It is an aquatic floating herb, common in large ponds, grown for the edible fruits (sanghara). The submerged stem bears dimorphic leaves ; the floating leaves form a rosette and leaves are rhomboidal, supported by the spongy inflated leaf-stalk while the submerged arising in pairs at the nodes are root-like, pinnatipartite, with filiform segments. Flowers solitary, axillary. Fruit a large obovoid bony quadrangular nut with 2-4 spines at the angles (Fig. 3.16)

Potamogeton crispus (Fig. 3.17). A fresh-water submerged herb, with slender, compressed stem and thin submerged leaves, which are distichous, 1-4 in. long and 1/3 in. broad, sessile, semi-amplexicaul, narrowly or broadly lanceolate, crisped, serrulate, 3-nerved translucent. Flowers small, bisexual arranged on a long curved peduncle, which tapers upwards.

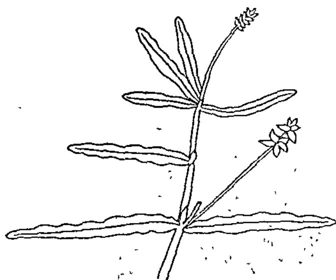


Fig. 3.17. *Potamogeton crispus*

Potamogeton pectinatus. A fresh-water submerged herb, with densely branched filiform stem. Leaves are thin, filiform

about 3-6 in. long and 1/10 in. or less broad, opaque, 1-3- nerved, margin slightly thickened or recurved. Peduncle long and filiform ; flowers few (Fig. 3.18).

Zannichellia palustris. A fairly common submerged plant in the

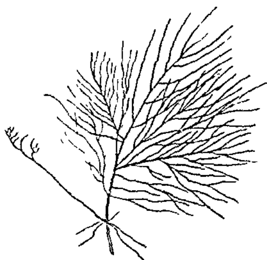


Fig. 3.18. *Potamogeton pectinatus*

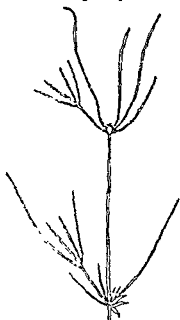


Fig. 3.19. *Zannichellia palustris*

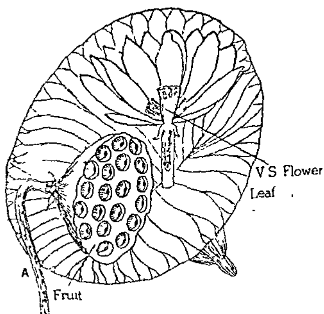


Fig. 3.20. *Nelumbium speciosum*

ponds, with slender root-stock and filiform stem. Leaves are linear and 1/2-3 in. long and 1/12 in. or less wide, crowded at the nodes, with a stipular sheathing base. Flowers minute, unisexual, a male and female enclosed in one membranous leaf-sheath (Fig. 3.19).

Marsilia quadrifolia. A common water-fern, with a slender creeping rhizome, showing distinct nodes and internodes. From the ventral surface of the node arise one or more adventitious roots, while long-stalked, quadrifoliate compound leaves are borne alternately on the upper side. The petiole shows marked adaptation to varying environments. It is long, slender and weak in aquatic condition but is short, stout and thick when the plant grows on moist land. Aerenchyma is plentiful in rhizome, petiole and lamina. Fertile plants bear sporocarps which are small, flat, bean-shaped structures.

Utricularia (Bladderwort). It is a submerged aquatic or marsh-plant, often found in standing water, lacking in nitrogenous salts. The plants are rootless, with slender stem which bears finely divided leaves. Some of the ultimate leaf-segments are modified into peculiar bladder-like structures, borne on small stalks. These bladders are small, hollow chambers meant for catching insects. Flowers are borne on long racemes, projecting above the water.

Nelumbium Speciosum (Lotus or Kanwal). It is a common water plant, often cultivated in big ponds for its rhizome (Bhen) and seeds which are edible. The rhizome is stout, elongated and creeping, containing hollow air spaces. It is rooted in the mud at the bottom of the ponds by numerous adventitious roots. Leaves are large, 2-3 ft. in diameter, raised high above the water, peltate. The petiole may be smooth or bear scattered prickles. Flower 4-5 in. in diameter, white or pink (Fig. 3.20). Fruit etaereo of



Fig. 3.21. *Nymphae lotus*

achenes, achenes embedded in an obconical spongy torus (**Kol chapni**).

Nymphaea lotus (Blue water lily—**Nilofar**). A perennial herb of shallow water with a creeping root-stock, rooted in the mud by adventitious roots. Leaves radical, 6-12 in. across, floating, borne on long, cylindrical submerged petioles, about 7 in. long, sharply sinuate toothed, downy and mostly purple beneath, sagittate and entire when young. Flowers 4-10 in. across, white or pink (Fig. 3.21).

QUESTIONS

1. Describe the morphological and physiological peculiarities of xerophytes. Give familiar examples.
2. Describe with examples the various types of adaptations met with in xerophytes for escaping and evading drought.
3. Describe the form and structure of plants growing in deserts. What peculiar features have helped them to succeed in such situations?
4. Name the xerophytes of your locality and describe the special morphological and anatomical characters of each.
5. State with figures and examples the various features of aquatic vegetation comparing them with those of marsh vegetation.
6. Describe the vegetation of a fresh-water pond or lake with which you are familiar. Describe the form and structure of these plants and adduce evidence in favour of adaptation to environment.
7. Write notes on the following :—
   Halophytes ; Alpine plants ; Bog plants ; Epiphytes.
8. How is it that seashore plants show xerophytic structures in spite of plenty of moisture in the soil and air?

4

PLANT COMMUNITIES AND PLANT SUCCESSION

PLANTS usually do not live alone in nature. In any particular area many plants belonging to one species, or more often to several species, live together forming small or large groups. Such an aggregation of plants having mutual relationships among themselves is called a **plant community**. Trees growing together in a forest with the ground flora form a community. Lichens and mosses growing on a rock; savannah with tall grasses and scattered trees ; a mat of algae on a pond or lake are all examples of plant communities of different types. The diffeient members of a plant community influence one another and also interact with the environment. In any particular habitat, the environmental conditions are uniform and only those plants will be associated together that are adapted to the conditions of the environment. In other words the various kinds of plants that require the same type of environment are habitually found living together in the same community. In a community, plants of one or more species are more prominent than the others because they are the tallest or largest and are present in considerable numbers. They largely control the environment and so determine what other species may grow in the community. These are called **dominants**. In a forest the dominant species are trees. A community may be open or closed. In the former, the plants grow quite apart from one another leaving bare areas where new species may arrive and settle. In a closed community, the growth is dense with little space between the members of the community for the entry of invaders.

MUTUAL RELATIONSHIP AMONG PLANTS

Competition. Plants growing together in a community influence one another directly or indirectly in a number of ways. *The foremost among such influences is competition.* The members of a community compete with each other for factors of the environment, like light, water and mineral nutrients. This competition is more pronounced if the demands exceed the supply. Competition among members of the same species, or intraspecific competition as it is called, is very acute for the simple reason that, being alike, their demands on the environment are identical. If the supply of water or nutrients or light is not sufficient for all the plants, the result will be poor growth, followed ultimately by the elimination of the weaker individuals. In the forest, thinning reduces competition and increases the yield of lumber. *For the same reason, removal of weeds from a cultivated field* gives more and better crop.

Stratification. Among plants of different species which do not have identical requirements, competition will not be so great. A rapid growing and tall species soon outgrows a short sized one. The latter, shaded by the former, can survive only if its light requirements are not so great. In this way *stratification* develops in a vegetation. Species that [illegible] and characterise the comn[illegible] Stratification occurs not only among the trees but may also be seen among the shrubs and herbs, since some may be tall and so [illegible] mosses, lichens an[illegible] be[illegible] by [illegible] jeopardise the continued dominance of the trees by offering compe- [illegible] seedlings are worsted [illegible] from the [illegible] e only if [illegible] ll strata of [illegible]

Dependencies. Some members of a community are dependent upon the others for their survival. Most of the thallophytes, *liverworts and mosses, ferns* and their allies, and some higher plants thrive in the moist and shady conditions met with on the forest floor. Removal of the dominant trees would result in the

disappearance of such dependent species. The same is true of epiphytes which are conspicuous in a tropical or sub-tropical forest. Fungi, both parasitic and saprophytes, are abundant in the forest soil. They are dependent upon the roots of the forest trees and on the rich humus that is found on the forest soil. Some fungi form mycorrhizal association with the roots of vascular plants.

THE EVOLUTION OF PLANT COMMUNITIES

If a cultivated field is neglected and not sown with crop, it is covered by a growth of annual weeds in the first year, followed by perennials the second year, and a community of perennials thereafter. In a forest, the herbs are soon replaced by woody plants. Such vegetational changes, occurring in a definite sequence, take place after any disturbance of natural vegetation—such as cultivation, lumbering or fire. It thus comes about that all plant communities have their origin ; they develop and finally mature. The origin of a commun [illegible]
organs (gemmules) li [illegible]
migration from old [illegible]
water or animals. [illegible]
is not favourable.. [illegible]
germinate in the new area and some of them grow into mature plants. These new arrivals from outside are called pioneers. These reproduce and multiply. T [illegible]
area by the pioneers. The [illegible]

[illegible]

results in competition for food, light and space, especially if the plants are close together. In this struggle, which is both inter-

changed conditions become less favourable for the early pioneers and more favourable for new invaders. The pioneers are thus replaced by new plants. These undergo the same process, modify the environment in their own way and may, in turn, be ousted by new invaders adapted to the changed conditions. Thus, shrubs may replace herbs and may, in turn, be ousted by trees.

In this way, a gradual but sure process of evolution of plant *community takes place as a result of the phenomena of migration,* ecesis, colonisation, aggregation, competition, invasion, reaction and interaction described above. Ultimately, the environment becomes stable because it cannot be modified indefinitely. It is now the climate that determines what will be the final type of vegetation—herbs, shrubs or trees. The *vegetation that develops ultimately* will be more or less permanent and will be in equilibrium with the climate. This is the highest type that the habitat can support under the prevailing climate and is called the **climax vegetation**. *The dominant species of a climax community* are nearly in complete harmony with the environment so that the community is relatively stable and will not change so long as the climate and physiographic factors remain the same. Moreover, *these dominant species are in complete control* of the environmental factors such as light, space, humidity, nutrients, etc. so that successful invasion by new species is mostly out of question. The result is that in a climax community the *number* of species is not large. *In any case, it is much smaller* than in some of the intermediate stages.

PLANT SUCCESSION

The plant communities that occupy a new area *are constantly* changing community. The vegetatio as an individual plant or ultimately matures. This process of evolution of plant *communities on bare areas* from birth to maturity is called **plant succession**. An area to be occupied with life starts as a lake to be filled in with soil, or a mountain of rock to be eroded into soil. The same area is eventually occupied *successively by a series of different plant communities* till a final or climax stage is developed. The intermediate stages in the process of plant succession are called seral communities and together constitute a sere. Successions beginning

in watery habitats (ponds, lakes, marshes) are called **hydrarch** and the different stages of development constitute **hydrosere.** Succession beginning in saline water is **halosere.** Successions beginning in dry situations are termed **xerarch,** and the different stages of the 'sere' constitute **xerosere.** Two types of xeroseres are distinguished, namely **lithoseres** originating on bare rocks and **psammoseres,** occurring on sand.

The bare area on which succession begins may be primary or [illegible] which no plant life grew [illegible] by recession of ice, a new island, newly-deposited volcanic ash or rock ; a secondary bare area is one on which plant life once grew but has now been destroyed by lumbering, fires, floods or by other causes. Seres on primary areas [illegible] subsere [illegible] and [illegible] sandy rock or water. The above facts lead to the following classification of seres :

Priseres :	*Subseres :*
Hydrarch	Hydrarch
Hydrosere	Xerarch
Halosere	
Xerarch :	
1. Psammosere 4 3.- oxylosere - on	
2 Lithosere.	

It may be mentioned that the climax vegetation in any area is ultimately determined by its climate. The climax community throughout a climatic region is, therefore, the same whether it begins as a xerosere or a hydrosere. Typical examples of plant successions are described below.

A HYDROSERE

A hydrosere may begin in a pond or a lake. The water is deep in the middle and becomes progressively shallow towards the shore. The various stages and processes that lead to the development of a climax community in such a situation are briefly described below :—

1. Submerged stage. The area of the lake where the water is more than 10 ft. in depth is almost without any flowering plants. Only algae grow here. Where the water is less than 10 ft. deep, may be found entirely submerged plants and free-floating plants

that are not rooted at the bottom. These are represented by *Potamogeton*, *Hydrilla*, *Vallisneria*, *Utricularia*, and *Zanichellia*. Submerged *Ranunculus* and many algae like *Chara* fill the water more or less completely with tangled vegetation. These are the pioneers of the hydrosere. The vegetation affects the habitat. The soil particles which were eroded from the shore are floating about

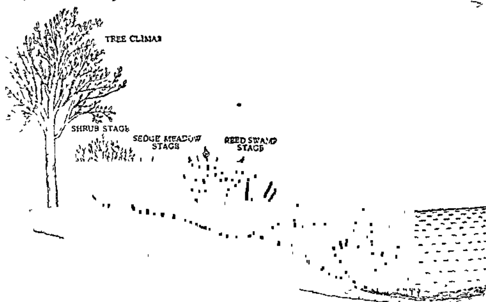


Fig. 4.1. Succession from a pond

in the muddy water. These are caught by the plants and deposited around them at the bottom of the lake. Some plants die; their [illegible] are converted into humus which also settles down and binds [illegible] s process of building the lake bottom [illegible] shallow and less fit for the submerged [illegible] the new invaders.

[illegible] a result of the processes resulting in [illegible] ibed in the preceding paragraph, the submerged plants move into deeper water; the area once occupied by the submerged plants is now invaded by species of floating plants, especially where the water is only 5 to 10 ft. in depth. These plants root at the bottom but have stems or petioles which rise nearly to the top of the water so that their leaves float at the surface. These plants migrate from shallow water mainly by means of rhizomes. The characteristic plants of this stage are species of *Nymphaea* (water lilies), *Potamogeton* (pondweeds), and *Ranunculus aquatilis* (water crowfoot) and some unattached floaters, such as

Lemna (duck-weeds) and *Eichhornia* (water hyacinth). The broad leaves of many of these plants cut off light from the submerged plants which, finding the conditions unfavourable, must migrate to deeper water. These plants continue further the process of building up of the lake bottom with the result that the water becomes too shallow and unsuitable for the floating species which would disappear.

3. Reed Swamp Stage. The water is now only 2 to 3 ft. and at most places less than 1 ft. in depth. Invasion now becomes possible for marsh plants such as *Typha* (cattail) intermingled with *Rumex*, *Eclipta* and *Sagittaria*. These plants are rooted at the bottom and are partly submerged but their shoots extend well above the water. They cut off light from the floating plants which now finding the habitat less favourable migrate into deeper water in the wake of submerged plants. These plants make the water still shallower by the settling down of sedimentary material and the deposition of plant humus. The habitat is consequently made unfit for the plants of the reed-swamp stage and favourable for the marsh-meadow stage.

4. Marsh Meadow Stage. The substratum now changes to a marshy soil with water table just at the surface or the soil may sometimes be covered with a few inches of water. Such a habitat is too dry for the plants of the preceding community and is invaded [illegible]
ing [illegible]
They [illegible]
soil [illegible]
plan [illegible]
[illegible] such a soil. These are gradually
[illegible] trees.

5. W[illegible] moist climate, the next stage is [illegible] and trees. The pioneers of this will be those that can tolerate partial water-logged conditions around their roots. These woody plants react upon the habitat like their predecessors, by casting shade and making the soil dry by their vigorous transpiration and catching wind-borne soil and accumulating plant debris. The previous occupants now disappear, being replaced by shade enduring herbs which grow among the trees and shrubs.

6. Climax Forest. As humus accumulates, bacteria and

other micro-organisms begin to thrive in the soil making it richer. Other trees now make their appearance. These react upon the soil. Under their canopy the air is humid but their shade will make conditions unfavourable for the seedlings of the pioneer sun-loving trees. After a few generations, the pioneers will be replaced by the trees of the most tolerant (shade) species.

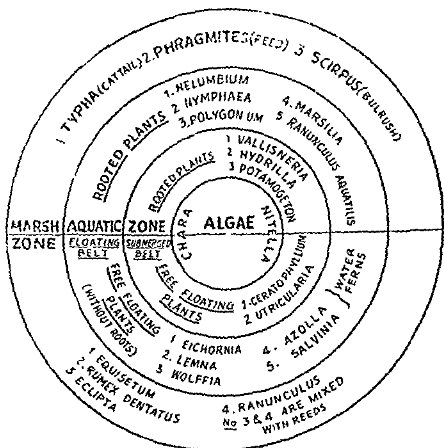


Fig. 4.2. Zonation about a pond

Thus, the area once under deep water becomes finally transformed into a forest. The whole process of development may be studied about lake margins where each stage may be seen as a definite zone as illustrated in figure 4.2. It should be remembered that the nature of the climax community will depend upon the climate. A forest community will develop only if the climate is moist. In dry climates, the climax community may be a grassland or some other xeric community.

A XEROSERE ON BARE ROCK

1. **Crustose-Lichen Stage.** The rock habitat is extremely xeric. Water and nutrients are extremely scarce and the conditions are aggravated by exposure to sun and wind and extremes of temperature. The first pioneers on such a habitat are the crustose lichens. They are very slow growers and can stand extreme desiccation. Whenever there is rain, they can absorb water like a sponge and flourish very rapidly. Migration takes place by lichen fragments or spores. The lichens secrete acids that slowly corrode and decompose the rock, making it rough.

2. **Foliose-Lichen Stage.** The change in the rock made by crustose lichens makes possible the growth of some xeric foliose lichens. These occupy the depressions in the rock and other weathered portions. Their expanded thalli overshadow and gradually replace the crustose liche [illegible] Water and humus collect [illegible] into the rock. Gradually, [illegible] ing of rock particles, rem [illegible] This prepares the way for xerophytic mosses.

3. **Moss Stage.** The accumulation of soil and some humus in the rock crevices makes the substratum fit for invasion by xerophytic mosses. Their rhizoids compete with the lichens and their erect stems overshadow the latter. They are as drought enduring as the foliose lichens and sometimes the two occur together or the moss may even come earlier. Fruticose lichens like *Cladonia* accompany the mosses and with them shade the foliose forms which are worsted in the competition and disappear.

4. **Herbaceous Stage.** The mosses increase the amount of the soil, and the death and decay of the older mosses often produce a mat on the rock surface. This mat has great water-holding capacity. Many herbs, first short-lived annual and later biennial and perennial, and xerophytic grasses make their appearance. The [illegible] the process of rock disintegration. [illegible] humus due to the death and decay [illegible] from the soil decreases and humidity increases.

5. **Shrub Stage.** Xeric shrubs now appear. The herbaceous plants of the preceding stage, now shaded, tend to disappear. The roots of the shurbs further corrode the rock which is now more or less completely covered with soil. The soil is further enriched by

humus formed from fallen leaves and twigs. The soil is shaded and evaporation from it reduced. Wind movement is retarded and humidity increased. All these conditions are favourable for the growth of trees and unfavourable for the former possessors of the land which disappear.

6. Climax Forest. The *first species of trees to appear are* xeric. Their growth is stunted and they are far-spaced. Their seedlings are shade intolerant. More soil is formed from the [illegible]

shrubs and earlier trees give place to more shade-tolerant and mesophytic *species of trees. A new herbaceous and shrubby vegetation,* adapted to the humid air and a moister and richer soil, develops in the shade of the forest floor.

From the two examples of succession described above, it will be noted that succession is convergent. Whatever the condition of the initial habitat, reaction tends to make it favourable to more plants by reduction of extremes, which is always reflected in improved moisture conditions. Thus, xeric habitats become moister and hydric ones become drier as succession progresses. Beginning as a hydrosere or a xerosere, the succession in the cases described above has culminated in a mesophytic forest. The deciding factor is the climate. Depending upon the climate, primary succession may lead to a meadow in place of shrub and tree stage. This is common in drier areas where various grasses make up the climax vegetation.

It will also be seen that a succession, whether a hydrosere or a xerosere is more or less characterised by a similar series of stages. These stages are (1) nudation, or the formation of a bare area, (2) migration and colonisation, (3) ecesis *i.e.* the establishment and maturation of the colonising species, (4) aggregation, (5) reaction, (6) competition, (7) stabilisation and (8) climax.

From the above account one may conclude that succession is a developmental process in which an area is the scene of several waves of plant populations, coming one after the other. Each wave occupies the habitat for some time. It begins slowly, then increases rapidly and finally declines and disappears. During this time it is in possession of the habitat, the plants of each wave profoundly influence the habitat, making it less fit for their own

only has a uniform physiognomy but is also uniform in its floristic composition, at least with regard to the dominant species. Each association has two (rarely one) or more dominant forms. Thus, in the temperate forests of Western Himalayas we have deodar—blue pine (*Cedrus deodara—Pinus excelsa*) and at higher altitudes spruce—silver fir (*Picea morinda—Abies pindrow*) associations. Similarly, in the Eastern Himalayas, the tropical zone which extends from the plains up to an altitude of 2,500 ft. is characterised by *Shorea robusta—Terminalia* association and in the lower temperate zone we have oak—michelia association and at higher altitudes we have *Abies webbiana—Picea spinulosa* association.

An association is characterised not only by a uniform physiognomy but also by its almost uniform floristic composition. at least with regard to dominant species.

Consociation. Associations usually have several dominants. Consociation is a smaller unit of a plant association characterised by a single dominant species. An association, therefore, can have as many consociations as there are dominant species. Some associations have but one species. In such cases the term consociation has the same meaning as association. Thus, in a coniferous forest we may have communities dominated by *Abies pindrow*, *Picea morinda* and *Pinus excelsa*. Each of these communities is a consociation.

Faciation. Portions of associations which are characterised by two or more dominants, all of them having the same physiognomy are called faciation. The association in such cases is composed of its various faciations. Faciation and consociation are both subdivisions of an association. The only difference is that the former is made up of two or more dominant species, having the same growth habit as the association, and the latter is composed only of one dominant species. Thus, the broad-leaved forests of Western Himalayas are an association of many species of oaks, walnut, maples and horse chestnut. The part of the association dominated by a mixture of *Quercus dilatata* and *Q. incana* is a faciation, whereas regions dominated purely by one of these would form *Q. dilatata* and *Q. incana* consociations.

Society. Society is a part of an association (or consociation or faciation) characterised by one or more sub-dominant species. Subdominants are species of different growth habits from the dominants. Thus, in a forest the subdominants are shrubs, herbs or cryptogams and in a grassland they are herbs or low shrubs. The

term society, therefore, applies to ground flora communities.

The terms used above, association and consociation, etc. refer only to climax communities and not to seral communities and most of them end with the suffix —*ation*. Terms for the corresponding seral communities end with the suffix —*cies*. These terms are *associes*, *consocies*, *facies*, and *socies*. Thus, reed-swamp is not classed as an association but an associes.

The classification of plant communities given above is based on the **monoclimax** hypothesis of Clements which postulates that in a climatic region only one climax is possible. Contrasting with this is the **polyclimax** conception according to which the vegetation of any large area may consist of more than one climax determined by several factors of the environment, namely climatic, edaphic and physiographic. The edaphic climaxes are the result of soil conditions. Physiographic climaxes are the product of local environment associated with peculiarities of topography. Halophytic climax may occur in maritime situations where only salt tolerant species can survive. All these climaxes occur in the same climatic zone. The major unit of vegetation under this system is not formation but association.

ENDEMIC SPECIES

Ordinarily, plant species are fairly widely spread because they possess adequate contrivances for dispersal of their fruits and seeds. In some cases, however, plants belonging to a species are restricted to comparatively small areas. This may be a district, a valley, a hill or an island. Such species are described as **endemic**. A classical example is a living species of *Metasequoia* (gymnosperm) which is confined to a single valley in China. Another well known example is the red wood tree *Sequoia sempervirens* which is confined to the coastal valleys of California in the U.S.A.

Endemism is the result of failure on the part of a species to disseminate its propagating organs like the seeds and fruits. This is due to the existence of great barriers to its spread like high mountain ranges, large deserts or great expanses of water. A species may not have spread because it is comparatively young and had not had enough time to spread. In most cases, endemic species *represent the last remnants of a group which is becoming extinct*, as in the case of the Chinese *Metasequoia*. The great majority " endemic species are of this type. They have many relatives .. ..

the fossils as in the case of *Sequoia*. They have little variability due to poor mutability and are adapted only to a particular environment. Even if they migrate to new areas they fail to establish themselves because they fail to adapt themselves to the new environment. Only variability based on mutations can bring about such adaptedness.

Oceanic islands are rich in endemic flora. These islands are isolated from the rest of the world by large expanses of water. The plants fail to cross these water barriers and to migrate outside their original habitat. No outside factors or influences operate to bring about their migration. The result is isolation from the rest of the world. The flora of Hawaii island mostly consists of endemic species. The genus *Wielandia* is endemic to the Seychelle island. It is an isolated island with large oceans separating it from other islands and continents. The fruits and seeds of the plants possess no adaptation for dispersal by water over long distances. *Ginkgo biloba* is endemic in parts of Japan and China. In India endemic species are met with in the high altitudes of the Himalayas, for example species of *Potentilla, Saxifraga, Primula, Corydalis*, and *Anemone*. The high mountains prevent their migration.

QUESTIONS

1. What is meant by a plant community? Give examples from your observation?
2. How is it that there is a tendency for an orderly sequence of communities leading to a climax community? What is the climax community in your region?
3. What factors determine the plants that will survive competition and become dominant in a particular habitat?
4. What is meant by plant succession? Give an example each of a xerosere and a hydrosere.
5. Classify the various kinds of plant communities
6. How do different plants of a community affect one another?
7. Describe the zones of vegetation about a large pond. What are the causes of this zonation?
8. Discuss the factors that may prevent a given plant species from establishing itself in a particular region.
9. Distinguish between Formation, Association and Consociation. Give examples of each.

5

VEGETATION OF INDIA

An important aspect of plant ecology is plant geography which deals with the distribution of plants over the earth's surface. Plant geography is a very large subject and India is a vast country with a rich variety of climates and vegetation. Any description of the vegetation of India must necessarily be brief and incomplete.

CLIMATE OF INDIA

It is noteworthy that India experiences climates, varying from the equatorial to the alpine in character. Its vegetation consequently shows a great variety, ranging from the wet tropical forests, especially in the east and south, to a desert in the north-west. The chief controlling factors of the climate are rainfall and temperature. The rainfall determines the type of vegetation and the extent of its distribution. The climate also shows pronounced seasonal variations. This determines the floristic composition. There are four seasons in India as given below :

1. Winter season, from January to February.
2. Summer season, from March to middle of June.
3. Rainy season, from mid-June to middle of September.
4. Season of retreating monsoons, from mid-September to December.

The characteristic winter month is January with mean temperature about 50°F in the north, gradually increasing towards the south, being 75°F at Madras. Still lower temperature prevails in the hills, where increase in altitude is accompanied by a falling of the thermometer. Cold winds are common in this period. These are

usually dry, except in the north-west of India and the east coast of Madras where some rainfall occurs. The winter rains of the Punjab are important for wheat and barley crops. In the northern plains, frost is frequent and in the hills, hail at lower altitudes and sleet and snow at higher altitudes. Most of the trees of this region are winter deciduous and the ground flora is also scanty. Quite often, late snowfalls in hills are responsible for dry cold winds in the plains and prolong the winter.

The hottest *months are April and May in the east and* May and June in the west. At many places, the maximum temperature rises above 110°F. Scorching winds blow especially in the northern plain. In the north-western desert area, high velocity dust storms and whirlwinds are of common occurrence and shifting sand dunes are a common sight. These drought conditions are hardly favourable for plant growth and constitute a great danger to plant life.

The wettest months are July and August with some rainfall in September and October. Regions of heaviest rainfall are the west coast of Bombay, Bengal, and Assam and the Eastern Himalayas; heavy rainfall occurs in parts of Bengal, Bihar, Orissa and Madhya Pradesh and part of Uttar Pradesh, at the foot of the Himalayas; moderate rainfall areas are Uttar Pradesh, Delhi and the southern plateau; low rainfall areas are Punjab, Rajasthan and North Kutch.

The rainy season is the most favourable for plant growth. On account of high temperature, trees show maximum growth and the ground flora is luxuriant. Heavy rains in the hills and the melting of snow at the mountain tops sometimes cause disastrous floods in several parts of the country. These *inundate extensive areas in the* plains and are responsible for soil erosion.

India is divided into four climatic regions which correspond with the great rainfall divisions.

1. **Wet zone.** This is the region of *heavy rainfall, the* average annual rainfall exceeding 80 inches. The zone comprises (*a*) The western coastal part of Bombay, Mysore and Kerala, *i.e.*, the western slopes of what are known as the Western Ghats, (*b*) Assam, (*c*) Eastern half of Bengal, and (*d*) the terrai region of Uttar Pradesh. Natural vegetation is evergreen and semi-evergreen forest. There is almost no danger of drought but floods constitute considerable danger to crops.

2. **Intermediate Zone.** The rainfall is between *40 to 80 inches*

a year. This comprises the north-east plateau and middle Ganges Valley and includes S.W. Bengal, Bihar, Orissa, part of Madhya Pradesh, East Uttar Pradesh, N.E. Andhra Pradesh, the eastern slopes of Western Ghats and East Madras. The natural vegetation is deciduous forest. Most of the trees are leafless in the hot summer.

3. **Dry Zone.** The annual rainfall is between 20 and 40 inches. This comprises N.W. Madhya Pradesh, S.E. Bombay, including Gujarat, Eastern half of Mysore and Western half of

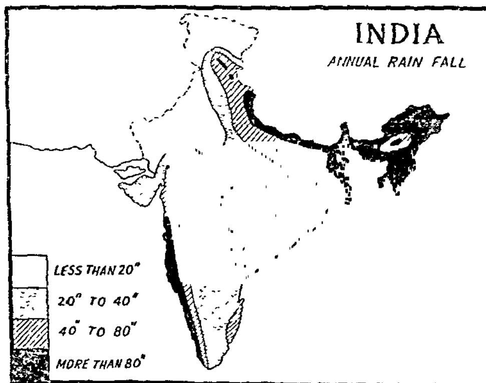


Fig. 5.1. Map of India showing annual rainfall

Andhra Predesh, Western Uttar Pradesh, Delhi and N.E. Punjab. Natural vegetation is thorny scrub land with dry deciduous forest occurring only in wetter localities.

4. **Arid Zone.** The annual rainfall is less than 20 inches. This comprises south-western part of Punjab, Rajasthan and North-west Gujarat. The natural vegetation is thorny forest with large areas of desert and semi-desert.

PLANT COMMUNITIES IN INDIA

The following is a brief account of the different types of plant communities met with in the different parts of India :

1. **Tropical Evergreen Forests.** Tropical (hot-wet) evergreen forests, also called rain forests, are characteristic of areas with annual rainfall exceeding 80 inches. They are found on the west coast extending from North Kanara to the south, and the eastern sub-Himalayan tract in Assam. In the luxuriance of vegetation, these forests are almost similar to the equatorial forests of the Amazon and the Congo Basin. The vegetation shows layering, the tallest trees sometimes attaining a height of about 150 ft. Climbers and tree epiphytes show prolific growth. There is also a very dense undergrowth of shrubs and these together with climbers make the forests sometimes impenetrable. The characteristic trees are *Dipterocarpus indicus* (**Gurjan**), *Hopea parviflora, Callophyllum tomentosum* (**Poon**) and *Mangifera indica* (Mango). Large tracts of these forests have been cleared by shifting hill cultivation or have been replaced by plantation of rubber, spices or betel palm.

2. **Temperate Evergreen Forests.** These are found in the hills of Nilgiris, Anamalai, Palni and Shevaroy in South India. They begin at about 5,000 ft. height. In the south, these forests are locally known as "Sholas". Here the characteristic trees are *Michelia Nilgirica* (**Pila Champa**), *Eurya japonica* and *Ternstroemia japonica* etc.

3. **Deciduous Forests.** These cover an extensive area of the country and correspond to the rainfall division with 40-80 inches annual rainfall. These forests occupy : (1) a strip along the wetter western side of the Deccan plateau, *i.e.*, Bombay, N.E. Andhra, (2) Madhya Pradesh, (3) Gangetic plain, and (4) considerable areas of the sub-Himalayan tract, extending from the Punjab in the west to the Assam Valley in the east. These forests are also known as the monsoon forests. They comprise the important Teak (*Tectona grandis*) and Sal (*Shorea robusta*) forests of India and produce some of the most important timbers of India. Many plants of the region shed their leaves in hot summer.

4. **Dry Deciduous Forests.** These forests occur characteristically in the Northern Punjab, where the rainfall does not exceed 30 inches and is often less than 20 inches. The tree growth is open with such species as *Acacia arabica* (**Babul**), *Acacia modesta* (**Phulai**), *Prosopis spicigera* (**Jand**), *Albizzia lebbek* (**Siris**) and

Dalbergia Sissoo (Sissoo or Shisham). Most of the trees are leafless in winter. The forests pass on to *Acacia* scrubland and desertic vegetation in drier regions.

5. **Coniferous Forests.** These occur in the temperate zone of the western and eastern Himalayas. In the western and central Himalayas these forests extend from about 5,000 ft. to about 11,000 ft. with abundant formation of conifers. The characteristic trees are Deodar (*Cedrus deodara*), blue pine (*Pinus excelsa*), spruce (*Picea morinda*), silver fir (*Abies pindrow*) and yew (*Taxus baccata*). In the Eastern Himalayas, the coniferous belt extends from 9,000 to 12,000 ft. The common coniferous species are · *Abies webbiana, Picea morinda, Larix griffithii* (Larch), *Tsuga brunoniana* (Hemlock spruce) and juniper.

6. **Alpine Forests.** These consist of dwarf trees and shrubs at higher altitudes in the Himalayas. In the west, it begins at 11,000-12,000 ft. and goes up to 15,000 ft. or sometimes higher. The characteristic trees are the high level silver fir, silver birch (*Betula utilis*), junipers and shrubby rhododendrons. The alpine zone in the Eastern Himalayas (above 12,000 ft.) is characterised by rhododendrons and junipers.

7. **Riparian Forests.** These grow on river banks and lands subject to periodical overflow or to percolation from rivers. The riparian forests of the Punjab are inhabited by *Acacia arabica, Populus euphratica* and *Dalbergia sissoo.* As you move away from the rivers, these trees gradually disappear and are replaced by *Tamarix dioica, Prosopis spicigera, Salvadora oleioides* and further away the leafless *Capparis aphylla* makes its appearance. Presently, the trees become sparce and bush-like and the landscape gradually merges into the desert.

8. **Mangrove or the Littrol Forests.** These forests occur on the coastal regions, *e.g.*, on the east and west coasts and the tidal swamps of the deltas of the large rivers, *e.g.*, the Gangetic delta and deltas of Mahanadi, Godavari, Krishna and Kavery. The region is composed of soft mud covered by mangrove forests of *Rhizophora, Sonneratia* etc. In these water-logged conditions, vegetation begins to decay and stink. Further inland where the area is inundated by tides are the tidal forests where trees like *Heritiera, Thespesia,* and palms and several shrubs grow. The Sundarban forests are of this category. They occupy largely the deltas of the Ganges and the Brahmaputra.

Extensive tracts of mangrove vegetation occur on the western coast, including Bombay and its suburbs and islands of Elephanta, Uttain, Uran, Mora, Gorai, Ghor Bunder and several others. The common species of mangrove trees are *Avecennia, Bruguiera, Cerisps, Rhizophora mucronata, Excaecaria, Agallocha, Sonneratia acida, S apetala* and *Aegioceras majus.*

9. Grasslands. Grasslands are not common in India. They occur in Khassi and Nilgiri hills. In most places in India, where the rainfall permits, forests abound. In many places the biotic influence of man has interfered with the natural growth of forests. The tree growth has been kept or rendered very open and the soil is covered with grass. An open forest with heavy grass cover is called savannah. Savannahs are found throughout the deciduous forest zone and in North Gujarat.

10. Arid or Semi-arid Vegetation. This occurs in regions *where rainfall is low both in winter and summer. The area covered* by the Indian desert runs through South Punjab, Rajputana, Kutch and North Gujarat. The annual rainfall at these places is less than 20 inches. Vegetation occurs only along the rivers in the form of riparian forests. The land away from the river courses and devoid of irrigation is mostly sandy and trees naturally do not grow there. Vegetation diminishes towards the desert region and almost disappears in the arid parts

11. Alpine Meadows. These are found at mountain tops above the timber line. The characteristic plants are drawf herbs which grow close to the soil and bear beautifully coloured flowers in early summer and autumn.

From the foregoing discussion it would be clear that there is *no such thing as the "Flora of India".* From the point of view of vegetation, India may be divided into the following regions: (1) Western Himalayas, (2) Eastern Himalayas, (3) North-Western dry region of Punjab and Rajasthan, (4) Gangetic Plan, (5) Central India, (6) West Coast, (7) the Deccan Tableland, and (8) Assam Valley.

THE WESTERN HIMALAYAS

This comprises the Himalayan Range including the Sub-Himalayan tract from Kumaon to Chitral. The rainfall varies from 40 to 80 inches, and in places it may be 100 inches or even more. But in the inner valleys and towards the north-west the climate is

dry.

In going up these mountains, one encounters variations in climate comparable to those encountered in going from the equator to the poles and these variations in climate lead to a recognition of more or less definite belts of vegetation and a rapid transition from one belt to another as the elevation changes. Three climatic zones, each with its characteristic vegetation, are recognised for the Western Himalayas. These are described below.

1. The Basal or Sub-montane Zone and the Outer Hills. This extends from the foot of the Himalayas to an altitude of 5,000 ft. The climate is tropical and sub-tropical with 80 to 90% rainfall from June to September followed by a cold winter and hot dry summer. In the lower tropical part of this zone is almost a continuous belt of Sal (*Shorea robusta*) in the eastern region forming a tropical deciduous forest. The tall straight trees with their dark-grey trunks form dense forests with a thick canopy of deep-green foliage. The undergrowth is rather scanty. The forest belt is interrupted in places by savannah in which the chief scattered trees are *Butea frondosa* (**Dhak**) and *Bombax malabaricum* (**Simal**). In the western region the Sal tree is entirely absent and Mango, **Simal** and **Kachnar** (*Bauhinia variegata*), **Amaltas** (*Cassia fistula*) and Neem are more common. In other places the following types of forests occur in this belt :—

(*i*) **Riverain forests** of *Acacia catechu* (**Khair**) and *Dalbergia sissoo* (**Shisham**) near the river banks

(*ii*) **Swamp forests** of *Eugenia jambolana* (**Jaman**), *Albizzia procera* (**Siris**), *Ficus glomerata* (**Gular**), *Pterospermum acerifolium*, *Cedrela toona*, *Trevia nudiflora*, *Putranjiva roxburghii*, *Celtis australis* and *Salix tetrasperma* with the cane, *Calamus tenuis*.

(*iii*) **Dry thorn forests** of *Zizyphus jujuba* (**Ber**) and allied species. The upper belt of this zone is occupied by mixed deciduous forests with several species of *Terminalia*, *Bombax malabarcium*, *Phyllanthus emblica* (**Amla**), *Odina Woodier* (**Jhigan**), *Hymenodictyon excellsum*, *Lagerstroemia parviflora*, *Steriospermum suaveolens*, *Holoptelia integrifolia*, *Cassia fistula* and many other species. These forests go up to 3,000 or 4,000 ft. The lower slopes are characterised by dense growth of the bamboo, *Dendrocalamus strictus*. At higher elevations, *Bauhinia retusa* and the giant liana *Bauhinia Vahli* are common. The tree-like *Euphorbia Royleana* is dominant on rocky cliffs and dry slopes. The **Chir** (*Pinus longifolia*) makes its

appearance at 2,500—3,000 ft. and higher up it forms extensive pure forests.

The forest is leafless from February to April. The undergrowth is rather scanty with a comparatively clean forest floor. Species of *Viscum* and *Loranthus* are common parasites. *Vanda cristata* and a few other orchids and *Peperomia reflexa* are a few epiphytic angiosperms. *Nyctanthes arbor tristis, Woodfordia floribunda, Bridelia montana, Rhus parviflora, Xanthoxylum alatum, Murraya Koenigii* are common pioneer shrubs along the streams. Other common shrubs are *Berberis, Rosa moschata, Rubus ellipticus, Principia utilis* and *Justicia adha toda.*

2. The Montane or Temperate Zone of Mixed Coniferous Forests. This zone extends from 5,000 ft. to about 11,000 ft. or a little higher. It has less rainfall and a lower mean temperature than the preceding zone. The total annual rainfall is above 40 inches and the winter precipitation is mostly in the form of snow. The vegetation is more luxuriant with abundant forests of conifers and deciduous broad-leaved trees.

The first among the conifers is *Pinus longifolia* which has persisted from the sub-montane zone. This continues up to 6,000 ft. but between 5,000 and 6,000 ft. it is gradually replaced by the blue pine (*Pinus excelsa*), which is the first characteristic conifer of this zone. The second characteristic conifer is Deodar (*Cedrus deodara*), which has almost the same range as the blue pine, but it often continues at higher elevations. A little above appears the Himalayan spruce (*Picea morinda*) which occurs from 7,500 to 9,500 ft. forming a distinct belt above the cedar. At about 8,000 ft. the silver fir (*Abies pindrow*) makes its appearance. The yew (*Taxus baccata*)) is common in the silver fir belt and the cypress (*Cupressus torulosa*) occurs only on the northern slopes at 8,000—9,000 ft. Thus, there are five coniferous belts. Each of the three upper coniferous belts has its characteristic oak which is the dominant broad-leaved tree. In the lowest, the white oak (*Quercus incana*) is associated with cedar ; in the middle, the green oak (*Q. dilatata*) intermingles with *Picea morinda* and in the upper belt along with *Abies pindrow*, the brown oak (*Q. semicarpifolia*) is the prevailing species. Other broad-leaved trees of the temperate zone are the maples (species of *Acer*), Indian horse chestnut (*Aesculus indica*), poplar (*Populus cilia*), elm (*Ulmus wallichia*), alders (*Alnus nepalensis* and *A. niteda*), birch (*Betula alnoides*) and the red flowered *Rhododendron arboreum*

and other trees. *Cornus capitata, C. macrophylla,* barberry, white rose and pomegranate constitute the flowering bushes. Ferns and epiphytes are abundant.

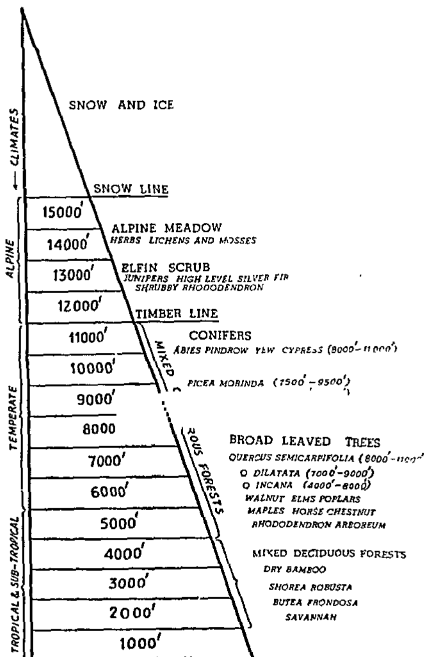


Fig. 5.2. Altitudinal zones of vegetation in the Western Himalayas

The most common shrubs of the temperate zone are *Salix, Rubus, Lonicera, Viburnum, Berberis, Indigofera* and *Principia.*

3. The Alpine Zone. Tree limit is reached at about 11,000 or 12,000 ft. beyond which are two zones of treeless vegetation: (1) sub-alpine shrub formation in the lower altitudes, and (2) alpine meadows in the upper altitudes. The characteristic plants of the sub-alpine zone are the high level silver fir, silver birch (*Betula utilis,*) junipers and shrubby rhododendron. These woody plants remain dwarf and shrubby forming what is known as elfin-scrub. The upper alpine region goes up to about 15,000 ft. and has a herbaceous vegetation of various kinds of grasses and herbs of a great diversity of beautiful colours of their flowers. The loss in the luxuriance of vegetation is compensated by the brilliance and profusion of bloom. In early summer and autumn, the alpine meadows present a sight of colours that cannot be matched anywhere else. The following list of flowering herbs of the alpine meadows will give some ideas of the colour festival:

1. *Potentilla argyrophylla*—Yellow to scarlet with all intergradations.
2. *Ranunculus hirtilis* and *Corydalis*—Yellow.
3. Species of *Polygonum, Sedum* and *Pedicularis*—Red.
4. *Saxifraga strachayi, Epilobium* and *Geranium reflectum*—Pink to red.
5. Species of Boraginaceae—Purple.
6. *Primula, Corydalis, Aster, Delphinium, Gentiana* and some *Labiatae*—Blue.
7. Crucifers and many compositae—White.
8. *Clematis orientalis* and involucres of *Euphorbia Tibetica*—Black.
9. *Anemone rivularis*—White.

An important feature of the alpine herbs is the cushion habit. The plants remain dwarf, and the stem branches, clothed with small densely arranged leaves, are packed together so tightly that they form a compact and more or less solid cushion. A single plant often covers a large area. Common Himalayan cushion plants are species of *Arenaria, Astragalus, Cragna* and *Androsace.* In others, the individual plants are very small with dwarf stems having short internodes, densely covered with small scale-like leaves. The plants are gregarious in habit, a single cushion being made of numerous plants. Above the alpine zone, the moun-

tain peaks are covered with perpetual snow and are devoid of vegetation.

THE EASTERN HIMALAYAS

The Eastern Himalayas extend from Sikkim to upper Assam, bounded on the north by Tibet and on the south by Bengal. This region is considerably more humid than the Western Himalayas. Like the Western Himalayas, it is divisible into three climatic and vegetational zones : (1) the tropical zone, (2) the temperate zone, and (3) the alpine zone.

1. Tropical Sub-montane Zone. This extends from the plains to about 5,000 ft. altitude. The vegetation comprises the following types :

(*a*) Sal forests including Sal savannah tracts in which the dominant grass is *Saccharum narenga.*

(*b*) Riverain forests of *Dalbergia Sissoo* and *Acacia catechu.*

(*c*) Mixed deciduous forests of *Terminalia* sp., *Lagerstroemia parviflora* **(Lendi)**, *Sterculia villosa, Bombax malabaricum, Anthocephalus cadamba* **(Kadam)**, *Schima wallichii* **(Chaillauni)** and many other species.

(*d*) Moist savannah forests consisting of stretches of tall savannah grasses with scattered trees of *Albizzia procera, Bombax malabaricum,* and *Bischoffia javanica.* The most common grass is *Saccharum procerum.*

(*e*) Evergreen forests of *Schima wallichii, Dillenia indica, Michelia Champaca, Eugenia, Echinocarpus,* Amoora and Cinnamon and many others. This region abounds in climbers and evergreen shrubs which form a dense undergrowth making the forest impenetrable.

2. Temperate Zone. This extends from 5,000 to 12,000 ft. altitude and has a much more humid climate. The forests of this zone can be divided into two belts :

(*a*) The lower belt of deciduous forests from 5,000 to 9,000 ft. comprising a number of species of broad-leaved trees. The common trees are the oaks (*Quercus lamellosus, Q. lineata* and *Q. pachyphylla*), *Michelia excelsa, Cedrela Bucklandia, Eugenia, Echinocarpus, Eleocarpus,* laurels, maples, alder, birch and many others.

(*b*) The upper coniferous belt extends from 9,000 to 12,000 ft. The common conifers are the silver fir (*Abies webbiana*), spruce

(*Picea morinda*), larch (*Larix griffithii*) and Himalayan hemlock (*Tsuga Brunoniana*). Besides these are the junipers, rhododendrons and dwarf willow.

3. **Alpine Zone**. This extends from 12,000 ft. upwards and is characterised by shrubby rhododendrons and junipers.

THE NORTH-WESTERN ARID LOWLAND (PUNJAB AND RAJASTHAN)

This region comprises the Punjab plain, Rajasthan, Kutch and North Gujarat. The northern part of this region, comprising the districts of Gurdaspur, Hoshiarpur and Ambala, has an annual rainfall of 20 to 30 inches. This occurs mostly in the monsoon months of July to September although some rainfall occurs in winter also. The south-western and south-eastern parts of the Punjab have an annual rainfall of less than 20 inches and merge into the Rajasthan desert in the south. October to February are the months of autumn and winter. The winter temperatures are low, often approaching the freezing point of water with consequent frost formation. Plant life becomes difficult. This is followed by the spring month of March when the temperatures are moderate and there is no rain. April to June are the months of hot, dry summer, the temperature sometimes rising above 110°F. Scorching dry winds blow and sometimes dust storms too. Sandstorms are quite common in the southern Punjab and Rajasthan. The climate is thus of a very xeric type and the conditions become worse as one moves from the north to the south. The soil is sandy and, except in the cultivated fields which are irrigated, the land dries up quickly after the rain. Vegetation is, therefore, poor ... ere are few species of trees, slightly more shrubs and ... nua ... ephemeral herbs. Trees are mostly confin ... ve ... where they form extensive growths for ... s ... common trees in these ... forests are ... and *Dal*

Cordia myxa and *Dalbergia sissoo* The last named tree is the most hardy and can subsist on soil with low water content. It is the common tree grown along the highways. The xerophytic shrubs of the Punjab desert are *Agave Americana, Alhagi maurorum, Calotropis procera, Opuntia dilleni, Euphorbia Royleana* and *Zizyphus nummularia*. Many annual and ephemeral species of herbs appear in early spring and in the rainy season when the conditions are comparatively favourable. The common xerophytic herbs are *Argemone mexicana, Carthamus tinctorius,* and *C. oxycantha, Solanum nigrum* and *S. xanthocarpum, Chenopodium album, Portulaca, Tribulus terrestris, Suaeda fruticosa* and *Salsola foetida*. The last named two species occur on saline soils.

The South-west Punjab merges into the hot dry desert of Western Rajasthan. This lies to the west of the Aravalli hills. In the south-eastern region of the Aravalli hills is the dry thorn forest consisting of *Anoguissus pendula, Bosewellia serrata, Sterculia urens, Acacia leucophylla, A. catechu, Zizyphus nummularia* and *Euphorbia nivulia*.

THE GANGETIC PLAIN

This extends from the Eastern Punjab to the Sunderbans in Bengal and passes through Delhi, Uttar Pradesh and a part of Orissa. The south-western part bordering on the Aravalli hills is semi-xerophytic and has the same vegetation as described in the preceding section. In the river country south of Jamuna are the open thorn forests of *Acacia arabica, A. leucophylla* and other species. The northern region is occupied by the Sal forest which is coextensive with the great Sub-Himalayan Sal belt extending from north Uttar Pradesh to Bengal. At the eastern end are the mangrove and tidal forests of the Sunderbans which occupy the tidal area close to the Gangetic Delta with such trees as *Rhizophora, Ceriops, Heritiera, Sonnertia* and *Avicennia*.

THE WEST COAST

This is a region of very heavy rainfall and lies between the Western Ghats and the west coast, extending from the south of Gujarat in the north to Cape Commorin in the south. Three types of forests occur in this region. These are the tropical evergreen forests, mixed deciduous forests, and temperate evergreen forests, with mangrove forests on the seashore.

1. The tropical evergreen or rain forests occur on the lower slopes of the Western Ghats facing the coast. The trees show luxuriant growth and attain great heights, sometimes reaching 200 ft. The forest floor is covered with a dense growth of shrubs. The forest also abounds in climbers and epiphytes. The forest is rich in the number of tree species, the common ones being *Dipterocarpus indicus, Hopea parviflora, H. Wightiana, Callophyllum, tomentosum, Cedrela toona, Callunia excelsa, Mangifera indica, Sterculia alata, Artocarpus hirsuta, A. integrifolia, Hydrocapus Wightiana* and many others.

2 The mixed deciduous or monsoon forests occur higher up in the mountain extending up to 5,000 ft. altitude. Most of the trees are deciduous and do not form dense forests characteristic of the tropical zone nor do they attain such great heights. Common tree species are *Tectona grandis* (Teak), several species of *Terminalia* and *Lagerstroemia, Dalbergia, Pterocarpus sp., Adina cordifolia, Grewia teliafolia*, and several bamboos.

3. The temperate evergreen forests. These occur at elevations above 5,000 ft. and are locally known as "sholas" The prominent trees are *Michelia Nilgrica, Eurya Japonica, Ternstroemia Japonica, Cardonia obtusa, Eugenia etc.*

4. Mangrove forests form large tracts on the coast of Bombay and its suburbs, including the Elephanta Islands, Uttain Island, Mora Island, Madh Island, Ghor Bunder and many other islands. The species of mangrove trees that occur here are given on page 102.

THE CENTRAL INDIA REGION

This region lies between the Ganges on the North and the river Godavari on the South and it comprises Madhya Pradesh, Orissa and the southern parts of Gujarat. The rainfall varies from 25 inches in the west and the central part to 70 inches in the east This region is divided into three vegetation zones: (1) The sal forest; (2) mixed deciduous forests; and (3) thorn forest.

1. Sal Forests These occupy the eastern part of Madhya Pradesh and Orissa

emblica, Odina woodier, Buchanania latifolia etc.

3. **The thorn forest.** This occupies the drier part in the central region with such common plants as *Acacia arabica, A. leucophloea, A. catechu, Balanites Roxburghii, Butea frondosa, Zizyphus zylophus, Z. nummularia* and *Prosopis spicigera,* the last occurring in very dry regions.

THE DECCAN REGION

This comprises the whole of the Southern Peninsula, south of the river Godavari except parts of the wet west coast. It is divided into two zones : (1) The elevated hilly plateau, and (2) the low Eastern Coromandal Coast.

1. **The Deccan Plateau.** The average altitude is about 2,000-2,500 ft. The rainfall is 20-30 inches and in the eastern part 30-40 inches with dry forests. Common plants are *Prosopis spicigera, Acacia planiformis, A. latronum, Albizzia amara.* Succulent *Euphorbias, Capparis divaricata,* and *C. aphylla* occur in more xeric places. In moister places, forests of *Hardwickia binata, Terminalia tomentosa* and *Anoguissus latifolia* occur. *Pterocarpus santalinus* abounds in hilly tracts.

2. **The Coromandal Coast.** The vegetation is dry evergreen forest. The rainfall is 40-50 inches. Besides the plants of the Deccan Plateau, such evergreen plants as *Strychnos nux-vomica, Eugenia sp.* and *Pterospermum,* are also found. In the drier parts *Randia, Flacourtia* and *Zizyphus* are met with. The sandy shore is covered with *Phoenix furnifera, Casuarina* and the grass *Spinifex squarrosus.* Halophytes occur in the eastern mangroves.

THE ASSAM VALLEY

It is a region of very heavy rainfall. Rainfall is about 80 inches and much more at some places. Cherrapunji has more than 400 inches of annual rainfall. In the valleys of the Brahamputra and the Surma outside the Sub-Himalayan regions, the common species are *Mesua ferrea, Artocarpus, Michelia champaca, Lagerstroemia flos-regina, Alstonia scholaris, Dillenia indica, Garcina sp., Corallia lucida, Aquillaria sp., Sterculia alata, Cedrela toona, Morus laevigata, Ficus elastica* and many others. *Dendrocalamus Hamiltonii* is a common bamboo. Canes, climbers and evergreen shr are abundant. On the river banks, *Albizzeia procera,*

malabaricum and *Lagerstroemia* are common. Sal forests occur in the Garo Hills.

In the hilly regions, the forests contain *Magnolia, Michelia, Acer, Prunus, Pyrus, Rhododendron arboreum, Bucklandia populnea, Alnus nepalensis, Betula alnoides* and many species of oak. Forests of *Pinus khasya* occur above 2,500 ft. especially at 4,000 to 5,000 feet.

QUESTIONS

1. Describe the vegetation of any mountain that you have climbed. Mention the dominant and subdominant species.
2. Describe the flora of your district or state and relate it to the ecological factors that operate there.
3. Write notes on the following :—
   Mangroves; Alpine meadow ; Timber line ; Elfin scrub ; Cushion plants.

6

APPLIED ECOLOGY

MAN exercises a very significant influence on the plants that grow in nature. Natural plant communities are permitted to continue if they are useful to him, are modified to serve his needs, or are destroyed to provide him with need for agriculture or industry. Quite often his activities result in modifying the environment.

Natural plant communities and their environments, especially the soil, are natural resources. It is necessary that their utilisation should be so regulated that they may continue to be available for our future generations
ples of plant ecolog
resources to the ful
continued use in th
communities like the forests and grazing lands, and to the cultivated plants. A knowledge of their ecology would ensure maximum continuous production from them.

FORESTRY

Unplanned and excessive felling of forest trees by man for a long time, especially during the last world war, to serve man's immediate requirements without regard to future needs was due mainly to the reason that man did not recognize the forests as a natural resource. As a result of the extensive lumbering, the total forest area in India showed a progressive decline. In 1950-51 the total forest area was 7·18 lakh sq. km. and in 1961-62 it had fallen to 6·95 lakh sq. km. The latter figure represents about 22 per cent of the total area of our country, whereas a healthy national economy requires that 33 per

cent of the total land area should be under forests.

Forestry is now a recognized subject and **silviculture** is an important branch of it. Silviculture deals with the establishment, development, care, and reproduction of forest trees. For the proper understanding and employment of silvicultural practices, knowledge of forest ecology or **silvics**, is necessary. Teaching of silvics is now a part of training in forestry. For some years now the Government of India has set up a central forestry commission and has laid down a national forest policy for the improvement of our forest wealth. Programmes for forest development include the development of economic plantations, rehabilitation of degraded forests, improvement of forest communications and roads, development of forest research, and forest protection measures. A special programme for fast-growing species suitable for industries like match, plywood, paper and pulp and boards has been launched. Between 1961-62 and 1964-65 an area of 53,580 hectares was brought under quick growing species and a further addition of about 28,700 hectares was made during 1965-66.

Development and control of forest communities require a knowledge of successional trends and the climax of the region. Such a knowledge points to the fact that the simplest form of management is one which least interferes with the natural development of vegetation. Sometimes it may be desirable to maintain a seral community indefinitely for the simple reason that the dominants of a certain successional community happen to include the most valuable trees. This requires the full appreciation and application of the principles of forest ecology. It should be obvious that it would be easier to maintain such a desired community if it is nearer to the climax and that best growth with the minimum of management is possible if a natural development of a climax community is permitted.

Forest management quite often involves other operations, like the control of soil erosion, watershed protection and game encouragement. All these require the adoption of scientific methods based on the correct understanding of forest ecology. Sometimes new tree species are introduced by man from outside. Their ability to grow successfully on the new sites is determined by their adaptation to the conditions of the environment and immunity to damage from insects and other animals, from disease, and from the climatic and edaphic factors of the new environment.

AGRICULTURE

In India, wheat, barley, gram, rape and mustard have been grown successfully as Rabi crops for a long time. Similarly, maize, sesamum, cotton and tobacco have been successfully cultivated as Kharif crops. This shows that the methods employed by the farmers, as well as the areas and seasons, were ecologically correct. Cultivated crops are as subject to ecological laws as are the native plants. A knowledge and application of the principles of the ecology of cultivated plants, which includes crop ecology, are essential for profitable agriculture in these days of planned economy.

Crop Ecology. The need for the study of ecology of a field of wheat, cotton or tobacco is as real as there is in a forest, because the cultivated plants are subject to the same laws of ecology as apply to the plants growing naturally. In the past the farmer has been drawing greatly on the soil for a reasonable return for his labour, unmindful of the fact that the soil is a natural resource which, apart from being used, must also be preserved and conserved. Such practices have resulted in the reduction of the natural fertility of our soils, erosion has ruined thousands of acres and reduced the productivity of many more, and water-tables have gone down to levels that pose a serious problem in areas of inadequate rainfall during dry spells. With the increased use of fertilizers, the development of high yielding varieties of crop plants, and modern mechanised methods, our yields have been progressively increasing. This increase in yield further reduces soil fertility.

Such negative trends must be remedied. Attention must be paid to the conservation of soil and control of erosion. Knowledge of crop ecology and its application are necessary so that we not only get the maximum yield of crops but also attend to the improvement of the soils so that they retain their fertility and ability to give continued high crop yields. With this end in view the following measures, based on the knowledge of crop ecology, must be adopted.

1. Highest yielding strains of suitable crop plants should be grown under proper conditions of cultivation and on the right sites.
2. Weeds must be eradicated. Correct steps in this direction are possible only after a study of the ecology of weeds.
3. Insect and animal pests, and diseases must be held in check effectively. The spraying of pesticides and fungicides from the air is economic and more effective and should be encouraged.

4. In areas where rainfall is inadequate or uncertain, irrigation of soil is necessary. Canal irrigation must be extended. Where it is not possible, arrangements for the supply of water should be made through minor irrigation schemes. Such measures should not be postponed till drought actually strikes the country. It is not wisdom that you begin digging a well when thirst overtakes you. The dangers from dry spells and want of irrigation are obvious from the famine conditions that developed in Bihar in 1967 and threatened Uttar Pradesh. Luckily, our government has not been idle and much has been done and still more needs to be done. During the second five-year plan period 36·42 lakh hectares of land were brought under irrigation through minor irrigation and in the third plan an area of about 52 lakh hectares has benefitted through minor irrigation. New wells and private tube wells have been constructed for this purpose. Ground water exploration is carried out in various parts of the country. The drilling of tube wells has been actively carried out in recent years, especially in Rajasthan, Kutch, Bihar, Uttar Pradesh, Punjab, Delhi, Gujarat, Madhya Pradesh and West Bengal. This work is progressing steadily. The Punjab Government provided 10,000 pumping sets to the farmers during 1967-68.

5. The use of manures and chemical fertilisers is necessary not only to increase crop production but also to maintain the fertility of the soil. Since 1964-65 large amounts of town-compost has been prepared in urban centres. Its production in 1965-66 was about 39 lakh tonnes. Sewage and sullage have been used for irrigation purposes. Night soil composting in rural areas and utilization of wastes like water hyacinth, green leaves and shrubs, tank silt and cattle urine for manurial purpose has been recommended. These potential soil fertilisers are at present not utilised or are only partially utilised.

The use of chemical nitrogenous and phosphate fertilisers is very important. Their use has been increasing steadily but it has not been possible to meet the full requirements on account of inadequate internal production and shortage of foreign exchange. Our consumption of nitrogenous fertilisers was about 6 lakh tonnes (N) in 1965-66 against 5·43 lakh tonnes (N) in 1964-65. India's present capacity of production of ammonia and urea is 585,000 tonnes of which about 90 per cent could be taken to represent actual production. New plants for the production of nitrogenous fertilizers

are being set up in various parts of the country and the Fertilizer Corporation of India hopes to achieve its target production of 19 lakh tonnes by the end of the fourth plan.

The consumption of phosphate fertilizers in 1964-65 and 1965-66 was 1·5 lakh tonnes (P_2O_5) per year.

Land Use. If all workable land were cleared of its natural vegetation and adopted to crop cultivation the result would be disastrous. Such a land, deprived of its natural vegetational protection would be very susceptible to erosion and would soon become a waste land. A proper use of land is determined by sound ecological considerations. The best arrangement would be to bring a minimum of well selected area under the plough with a maximum of natural vegetation. The natural vegetation, whether it is a grassland or a forest, should be protected and preserved.

Natural vegetation ensures that soil is being rebuilt and retained. It provides organic matter, regulates moisture conditions of the atmosphere and soil in a manner that man cannot duplicate, and provides food and shelter for wild life, which may effectively check and reduce plant pests.

A rational use of land will involve consideration of soil topography, exposure, and drainage in terms of the climate and cultivated crops it will support. Available areas on hilly land may be used for growing orchards, vineyards, pasture, and other crops without depletion or erosion of the soil. Stream banks are often used for grazing. This results in increased run-off of water and bank cutting. This can be prevented by planting, under protection, suitable species that can check erosion. Quite often the unproductive margins of fields are covered with hedge plants to reduce erosion and to provide cover for wild life. The ecology of planted species must be known as well as its effects on the crops beside it.

Land Management. Under this term are included all operations by which land is prepared for crops, their planting, harvest, and use. If a field is planted with the same crop, say wheat or cotton, year after year, the results will be far from satisfactory. The soil will be progressively depleted of the same mineral nutrients and will become infertile. There will be more diseases of crop plants and more insect pests than ever before. Growing crops on the principle of rotation, incorporating legumes in the rotation programme, with the addition of fertilizers is a better method of agriculture. This will give high and sustained yields, maintain

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soil fertility, and protect the soil from erosion. Growing mixed crops, which providing complete soil cover as in nature, would be more desirable.

PASTURES AND GRAZING LANDS

Pastures and grazing lands receive little or no attention with the result that they do not thrive. Quite often they occur in the form of natural cover on poor and neglected wastelands, that are not fit for crop cultivation, or on road sides. In India the total area under permanent pastures and grazing lands was 67 lakh hectares in 1950-51 and 140 lakh hectares in 1962-63. A large percentage of these occurs at the foot of mountains, on the fringes of forest or in open forest communities. They also occur as alpine meadows on the mountain tops and in valleys surrounded by mountains.

The maintenance and expansion of grazing lands is largely applied ecology. In this connection a knowledge of regional climaxes, with their grazing value, and the patterns of succession for each region is necessary. The quality and type of forage provided by each community have to be considered and also how they may be controlled or modified to advantage. The relationships of grasses and associated herbs have also to be studied. Quite often seeding is necessary for the proper development or speedy recovery of grazing lands to meet the needs of expanding dairying. Many species must be tested for palatability, yield, food value, and soil-binding properties.

The effects of grazing on community structure must be studied and grazing should be controlled with a view to permit the grazed land to return to normal. Attention must also be paid to the effects of drought as well as the rates with which grazing lands recover from drought. This makes it necessary to determine the water requirements of different species.

High yielding strains of fodder grasses have been produced in India. Among these are Pusa giant Napier grass with a yield potential of 3,000 mds. per acre and Anjan grass which gives a yield of 500 to 600 mds. per acre without special irrigation facilities throughout India. These were released by the I.A.R.I., New Delhi. Another promising variety in Napier Bajra hybrid released by the Punjab Agricultural University, Ludhiana.

CONSERVATION

This is concerned with the conservation of natural resources, like soil and soil water, for future needs. These and other natural resources, like vegetation and wild life, should be utilized in a judicious manner so that side by side with their utilization, they are retained and developed so as to ensure their continued availability to future generations.

The various measures which soil engineers and farmers have evolved for erosion control and soil building have been described in Chapter 2 of this book. It should not be understood that all those methods are applicable everywhere. They must be adjusted in terms of soil types and climate.

Great damage has been done to our land in the past due to erosion and extensive areas, which were once fertile, have been turned into wasteland. Since 1951 the Government of India has taken concerted action in the direction of soil conservation and reclamation of wastelands. During the third five-year plan period (1961-62 to 1965-66) an area of more than 40 lakh hectares benefitted from soil conservation as against 12·95 lakh hectares covered during the first and second plan periods (1951-52 to 1960-61). During 1965-66 an area of 86,900 hectares was brought under afforestation and pasture development, and an area of 30,352 hectares of ravine, saline, and alkali soils came under soil conservation schemes.

Continued agriculture, even in areas with adequate rainfall, creates water problems that did not exist before. The crop plants absorb large amounts of water from the soil with the result that the level of the water table in the soil is lowered. Where once streams were abundant and flowed throughout the year, now they are intermittent and summer water supplies are often low. In areas where the natural vegetation is removed for agricultural purposes, floods are of common occurrence in the rainy season. The rain water which used to soak into the soil when it had its natural plant cover now runs off rapidly producing floods which cause great damage to crops, land and property. Excess of water is as dangerous to plants as its shortage.

Attempts are now made to conserve, retain and store surplus water so that it may be available in times of need, so that water tables may be maintained at the proper levels, and so that flood waters may be controlled. To this end several projects have been taken up for the construction of dams, water reservoirs and flood

embankments and steps have been taken to protect water-sheds. A list of such projects is given below :

Gandak Project (Bihar) ; Kosi Project (Bihar) ; Kakrapara Project (Gujarat) ; Tawa Multipurpose Project (Madhya Pradesh) ; (5) Bhadra Reservoir Project (Mysore) ; Upper Krishna Project (Mysore) ; Malaprabha Project (Mysore) ; Nagarjunasagar Project (Andhra Pradesh) ; Tungabhadra Project (Andhra Pradesh and Mysore) ; Hirakud Dam Project (Orissa) ; Bhakra Nangal Project (Punjab, Harayana and Rajasthan) ; Beas Project (Punjab, Harayana and Rajasthan) ; Rajasthan Canal Project (Rajasthan) ; Chambal Project (Madhya Pradesh and Rajasthan) ; Ramganga River Project (Uttar Pradesh) ; Mayurakashi Project (West Bengal) ; Ganga Barrage Project for the preservation of the Port of Calcutta (West Bengal) ; Damodar Valley Project (West Bengal and Bihar). A brief account of the Punjab-Rajasthan projects is given below.

"A joint venture of Punjab and Rajasthan, the Bhakra Nangal Project is India's biggest multipurpose river valley scheme and was originally estimated to cost Rs. 175·60 crores. The estimates have now gone up considerably. It consists of a *226* metre high dam across the Sutlej at Bhakra ; 29 metre high Nangal dam ; 64 km. long Nangal hydel channel ;..... and about 1,104 kms. of canals and over 3,360 kms. of distributaries. Started in 1948 the project has been practically completed."

"The Bhakra canal system commands a gross area of about 27·4 lakh hectares, of which the cultivable commanded area is 23·7 lakh hectares. On full development an area of 14·60 lakh hectares is expected to be annually irrigated. In addition, about 14·60 lakh hectares will get increased water supply. An area of 13·02 lakh hectares in Punjab and Rajasthan received irrigation facilities during 1964-65."

"The Beas Project, which is a joint venture of the Governments of Punjab and Rajasthan, consists of two units, *viz.* (*i*) Beas-Sutlej link, and (*ii*) Beas dam at Pong. The former provides for a diversion dam at Pandoh, a combination of tunnels and an open hydel channel......"

Primarily intended for storing water for the Rajasthan canal, the project was intended to provide perennial irrigation to about 20·24 lakh hectares in Punjab and Rajasthan. The total irrigated land area in 1969-70 was 35 lakh acres.

"The Rajasthan canal project is intended to provide irrigation by flow supplies to about 11·6 lakh hectares in the district of

Bikaner alone, besides other areas in Rajasthan. It envisages the construction of a canal taking off from the Harike barrage across the river Sutlej and has been divided into two parts :

(a) Rajasthan feeder : 214·4 km. long, of which the first 179·6 km. lie in the Punjab.

(b) Rajasthan canal : 469·8 km. long lying entirely in Rajasthan.

To begin with, the Rajasthan canal is being fed by flow supplies from the Ravi and Beas rivers. Later, the flow supplies will be supplemented by stored waters from dams proposed to be constructed on these two rivers."

The project is now proposed to be executed in two stages. The first stage comprising the Rajasthan feeder and the first 196·3 km. of the Rajasthan canal, including take-off channels, was expected to be completed in 1969-70. The progress is slow and only 96 km. have so far been completed. The second stage envisages the completion of the remaining length together with the distribution system below Naushera branch. The Naurangdesar, Khetowal, Khodan, Zorawarpura and Rawatsar distributaries have been completed. Work on other distributaries is in progress. The total area irrigated by the Rajasthan canal system in 1968-69 was [illegible] lakh acres. The full development of this canal is the only answer to the recurrent famine problem in Rajasthan. The entire length of the canal and the feeder will be lined to save water losses through seepage.

LANDSCAPING

Plants beautify the environment in which they grow and determine to a great extent the landscape. They satisfy man's aesthetic taste and it is for this reason that they are cultivated, singly or in combination, in homes, parks and gardens and on the road sides. The successful growth of landscape plants is as much determined by ecological considerations as for the ones with plants growing naturally. In selecting plants for landscape designing careful attention must be paid to the requirements of the species used in terms of soil texture and structure, available water, temperature tolerance of shade and light, and competition. These and other factors operate to limit the range of landscape plants in different parts of the country in the same manner as they do in the [illegible]

natural plant communities.

Ne [illegible] the form [illegible] al colonie [illegible] oy natur [illegible] This [illegible] also t [illegible] process and, before that occurs, soil erosion sets in causing disruption of drainage, road blocks and similar difficulties. Artificial seeding and planting often become necessary to stabilize the soil. In so doing, one must keep in mind the question of succession and the possibility of harmonising the developing vegetation with that of the surrounding area.

PLANT INDICATORS

It was stated in the beginning of this book that plants growing successfully in any situation are in complete harmony with the factors of their environment. Different species differ in their environmental requirement and a species establishes itself and spreads where it finds the conditions suitable. The character and make up of vegetation is thus indicative of the integrated effects of all factors operating ir [illegible] of the relat [illegible] can [illegible] can [illegible] ional land use. In this way [illegible] woul [illegible] sites should be cultiv [illegible] as well as which crops [illegible] e more complete this k [illegible] be used, and the more certainly can land values be fixed for sale and taxation.

A few examples would illustrate the above point. A growth of tall and mixed grasses indicates that the soil is fertile and suitable for cereals and fodder plants. Areas covered by short grass have low soil water content and can be cultivated with crops having low water requirements, otherwise irrigation is necessary for cultivation. Where the natural vegetation is comprised of such plants as *Calotropis*, *Argemone mexicana*, *Agave* or *Opuntia*, the indications are of semi-desert conditions, both in the matter of climate and soil. Cultivation on such areas is a tough job requiring perennial irrigation and manuring of the soil. Plants like *Salsola foetida*,

Salicornia and *Suaeda fruticosa* are indicators of saline and alkali soils. Such soils are not fit for agriculture till the accumulated salts are removed. Rich growth of moisture-loving herbs, mosses, liverworts and lichens is an indicator of forest sites.

QUESTIONS

1. Write an essay on the practical applications of Plant Ecology to plant problems.
2. Of what use is the knowledge of plant ecology in (*a*) forestry (*b*) agriculture ?
3. Write notes on the following :—
   (*a*) Plant indicators
   (*b*) Conservation of water.
   (*c*) Crop ecology.

INDEX

PART II

GENETICS AND EVOLUTION

1

HEREDITY, VARIATION AND GENETICS

An important characteristic of all living things is reproduction. By this process, each individual transmits life to a succession of new ones, its offspring, and thereby maintains its continuity. There are two principal methods of reproduction, the vegetative or asexual method and the sexual method. In the former, a part of the body separates from the parent and under favourable conditions develops into a new organism complete in every respect. While this method is common in plants, it is very uncommon in the animal kingdom, being confined only to the simplest forms.

The prevailing and more important than this asexual method is the sexual method of reproduction. The essential feature of this method is the union of two sex cells called **gametes**. The result of this union, which in biological language is called **syngamy** is the formation of a single cell called **zygote**. The zygote later on develops into a new individual. The gametes are tiny bits of living matter, so small that in most cases they cannot be seen except with the help of a high-power microscope. An idea of the infinitely small size of the gametes may be obtained from the fact that all the male gametes which were responsible for the birth of more than two billion human beings of the world, when packed together, would make no greater bulk than an ordinary quinine tablet. The gamete is the only material thing that a parent contributes to each of its offspring. In other words, these gametes constitute the only physical link between one generation and the next. Everything that is transmitted by the parents to the offspring must, of necessity, pass across this extremely narrow bridge of gametes.

In the higher plants, the male gametes are produced in the pollen-grains and the female gametes in the ovules. When the female gamete is fertilised by the male gamete the result is the formation of a single-celled zygote. The zygote undergoes growth and develops into the embryo of the seed. By the same process of growth the embryo under favourable circumstances produces the new plant resembling in general form the parents which contributed the gametes In this way a zygote formed in the ovule of sunflower gives rise ultimately to another sunflower plant and that formed in a banyan tree gives rise to another banyan tree. What a contrast between the tiny one-celled zygote and the huge adult banyan tree that ultimately develops from it ! The proportion between the bulks of the two can be better imagined than described The increase is several hundred billion times. This increase takes place at the expense of a large amount of material taken from the outside. This material is obtained by the zygote first from the parent plant in which it develops and later, when it has grown into a small seedling, from the environment in the form of water and mineral salts from the soil and carbon dioxide and oxygen from the air. With the help of energy of sunlight these simple materials are changed into organic compounds which are ultimately incorporated into the body of the plant. A somewhat similar process takes place in the animals. A fertilized human egg cell is just large enough to be visible to a naked eye and weighs about 1/20 millionth of an ounce. Starting from this insignificant bit of matter, the body grows until it attains the adult size weighing 150 to 160 pounds. This is almost 50 billion-fold increase. The zygote grows first by the food that it obtains from the mother in whose body it develops and later, when it develops into a small animal, food is obtained from the plants or other animals that live in the environment. The food thus obtained undergoes profound chemical and physical changes within the body and is finally assimilated, that is, it is converted into cell material. In this way, an organism builds its body out of the food that it takes, each in a definite way and after its own pattern. The same kind of food results in the development of a banyan tree in one case and sunflower plant in another. The same is true of the different animals, for example, of dogs, cats and men. The result of food assimilation and growth in each case is the development of a body very much like those of the parents and other

ancestors of the developing individual. It is a significant fact that the outcome of growth and development depends very largely on the nature of the body, the zygote and the gametes which entered into its making and only secondarily on the food assimilated. This is the essence of **self-reproduction.** It is owing to self-reproduction or **heredity** that every form of life tends to produce individuals that are more or less faithful copies of itself. In other words, it is heredity which causes the process of assimilation to result in self-reproduction. It is due to heredity that a banyan tree produces seeds, each potentially a new banyan tree, and it is due to heredity again that always a sunflower plant springs from the seed of a sunflower and never a mango tree. The basic principle that 'likes beget likes' and that the distinguishing characters of a species are maintained generation after generation applies not only to plants but also to all animals and man. It is the fundamental law of life. Heredity, in short, is the tendency on the part of offspring to reproduce the characters of the parents.

However close may be the resemblance between individuals related by descent, it is never complete. An offspring is never an exact copy of its parents. Except in the case of identical twins, no two offspring of the same parents are identical. There are always small differences. Such slight differences are called **variations.** Variations may be due to environmental causes. These are called **modifications.** As a result of different conditions of the environment, for example food, light, temperature, etc., two individuals having the same heredity may become somewhat different. The other type of variation is hereditary, by which is meant that variation which is present from the time of birth and which is due to differences in the inheritance received from the parents. Among sexually reproducing organisms, no two individuals have the same heredities. The differences in hereditary constitutions are responsible for **hereditary variations.** These and environmental variations occur in nature side by side, so that some of the differences between individuals are due to environment and others are hereditary in origin. It is owing to hereditary variations that each individual is unique in itself and one can readily tell one person from another.

Heredity and variations go side by side and are the basis of evolution. That branch of biology which deals with the facts and laws of heredity and inherited variations is known as **genetics,** a

term first used by Bateson in 1906 for the study of the "physiology of heredity and variation". Genetics is the science which tries to explain why living things resemble their parents, and yet differ from them. It is the science which differentiates between what is inherited and what is not.

MENDEL'S PREDECESSORS

Our present knowledge of the phenomena of heredity has its origin in the work of Mendel (1865-66). But men all through the ages have tried to explain the causes of heredity. They were, however, ignorant of the basic facts of reproduction and their explanations were mostly based on heresay and superstition. Thus, from the time of Aristotle to the eighteenth century, the view was widely held that the mother furnishes inert matter and the father imparts the motion to the new life. Others thought that the parental "blood" mixed in the progeny so that the heredity of the offspring was a solution, or an alloy of equal parts of parental heredities Leonardo da Vinci (1452-1519) recognised that the male and the female parents contributed equally to the heredity of the offspring. According to Galton, the parents contributed one half each to the heredity of the offspring; the four grand-parents one-quarter each; the eight great-grand-parents one-eighth each, and so on. Even Charles Darwin accepted Galton's law of ancestral heredity.

Although the ancients carried out pollination in their economic plants, systematic experiments in plant hybridisation with a view to analysing problems of heredity were first carried out in the eighteenth century. The pioneer plant hybridiser was a German botanist, Joseph Kolreuter (1760-66). He experimented with crossing two species of tobacco by placing the pollen from one species on the stigmas of the other and arrived at the following conclusions :

1. The hybrids are usually intermediate between their parents in nearly all characters observed, such. for example, as size and shape of parts.

2. This indicated that hybrid offspring inherit equally from the pollen parent and the ovule plant. It made no difference in the appearance of the hybrid which of the parental plant was the pollen parent (male), and which the seed-parent (female), that is to say, in the case of plants the result of reciprocal crosses is usually identical.

3. Hybrids obtained from widely different species are partially or wholly sterile but often exceed either parent species in size and vigour of growth.

A later experimenter in this field was Knight (1759-1838). He observed that the hybrids were uniform in character and segregation of characters occurred in the second generation.

Another important figure among early hybridisers was John Goss (1822) of England who reported some interesting facts about inheritance in peas. He cross-pollinated two varieties of peas, one which had always borne blue peas and the other which had always borne yellow peas. All the seeds that developed were yellow coloured. The plants that grew from these yellow seeds were permitted to self-pollinate. The pods that developed contained a mixture of yellow and blue peas. Both these types of peas were planted. The resulting plants, when mature, were allowed to self-pollinate. When the pods developed, Goss observed as follows :—

1. Every plant arising from a blue seed produced pods containing blue peas only.

2. Plants arising from yellow seeds were of two kinds. Some produced pods containing a mixture of yellow and blue peas, some produced pods containing yellow peas only

Unfortunately Goss did not keep a statistical record of his experiments nor does he seem to have grasped their significance or attempted any interpretation of the results. That probably explains his failure to read the fundamental laws of inheritance which almost cried out to be discovered in his work.

Forty years later, a Frenchman, Naudin (1862) arrived at the following important conclusions as a result of his hybridisation experiments on plants.

1. Hybrids when repeatedly crossed with a parent, would be brought back to the form of that parent.

2. The potentialities of both the parents are present together in the hybrid.

3. When the hybrid forms ovules and pollen-grains, these potentialities segregate from each other. An ovule A of such a hybrid if fertilized by pollen of the parent plant A, will produce a plant of the parent type A.

4. The segregation applies to single potentialities or characteristics rather than to all the potentialities of a species at once.

The last two ideas of Naudin form the basis of Mendel's

laws. Naudin thus came very near to the facts of heredity but it was left to Mendel to enunciate the basic principles of heredity four years later. Like all great discoveries, the science of heredity was not made in a day, nor as the result of one man's work alone. Mendel added one final touch to the work of his predecessors as summarised by Naudin.

QUESTIONS

1 Define the following.
(*a*) Heredity (*b*) Variation (*c*) Genetics.
2 Give a brief account of the work done and the views on heredity upto the time of Mendel.

2

MENDEL'S LAWS OF HEREDITY

THE basic principles of heredity were formulated by Gregor Johann Mendel in 1865. Mendel was a monk in the monastery of Brunn, Austria (now Berne, Zechoslovakia). He had studied science at the University of Vienna and was working as a teacher of natural science at Brunn. This post he held till 1868 when he was appointed abbot of the monastery. In his monastery garden, he carried out his famous experiments on garden peas from 1857 to 1865. The results of these classic experiments and Mendel's conclusions, which are basic to the science of heredity, were published in the annual proceedings of the Natural History Society of Brunn, 1865, which appeared in 1866. Unfortunately, however, this remarkable piece of work which ranks among the outstanding biological contributions of all times was overlooked by the scientists of that time. The explanation often given is that the scientific world at the time was busy with the controversy raised by the publication of Darwin's book, *Origin of Species*. This seems hardly logical, for at that very time the biologists were striving hard for an explanation of heredity as an aid to understanding evolution, and a paper like that of Mendel should not have escaped their notice. The main reason for the neglect of Mendel's work appears to be that the biologists at the time of Mendel were unable to understand or appreciate his statistical approach. In any case, it is unfortunate that Mendel's carefully worked out explanation should have remained unknown for thirty-four long years.

Then, in 1900, three different men, who were working on heredity in plants independently arrived at the same conclusion which

Mendel had reached earlier. These men were Hugo de Vries in Holland, Karl Correns in Germany, and Eric Von Tschermak in Austria De Vries also unearthed Mendel's neglected paper and it came to be known that the laws of heredity had already been discovered and clearly stated many years previously by an obscure Austrian monk. The work of these men and later on of others showed that Mendel's laws applied not only to the garden peas but to other plants and animals as well.

MENDEL'S EXPERIMENTS

Mendel grew in his garden 34 different varieties of peas the seeds of which he had obtained from the local seedsman. He first made sure that every one of these varieties bred true to its type. For his experiments, he selected those varieties which contrasted sharply in certain definite traits. For example, he selected a tall variety (6—7 ft.) and a short one (¾—1½ft.), or a red flowering variety and a white flowering variety. Mendel adopted the following procedure in all his experiments. He crossed two plants which differed constantly *in one or several* characters and *planted the* seeds so obtained to produce offspri [illegible]

[illegible] least one set of characters. The process of crossing which results in the production of genetical hybrids is called **hybridisation**. The hybrids, on attaining maturity, were allowed to self-fertilize to produce the second generation. Before proceeding further, the meaning of certain terms commonly used in the explanation of such experiments must be clearly understood. The plants of unlike character with which the hybridisation is first made constitute the **parental** or *P* generation and the progeny of hybrids *obtained* from this cross is called the **first filial** or F_1 generation. When *the* F_1 hybrids are *self-fertilized* or *inbred*, *i.e.*, bred amongst themselves, the progeny resulting therefrom is called the second filial or F_2 generation. The subsequent generations resulting from self-fertilization are called F_3, F_4 and so on. When an F_1 hybrid is crossed with one of the *P* parents, the operation is called **back-crossing.**

As illustration, we will describe one of Mendel's own experiments. He crossed a tall variety of pea (*i.e.*, a pea plant, *all*

previous ancestors of which had been tall) with a dwarf variety (*i.e.*, a plant, the previous ancestors of which always had been dwarf). The resulting seeds, when planted, always produced tall plants (F_1). It made no difference whether the tall parent provided the pollen and the dwarf acted as the seed-bearing plant or *vice versa*. In other words, reciprocal crosses gave the same result. The character for dwarfness did not appear at all in the F_1 hybrid. There were no intermediates either. Now the question arose, what had happened to the dwarfness? Was it completely lost or was it only lying hidden in the F_1 hybrid? To find an answer to this problem Mendel permitted the F_1 hybrids to self-pollinate. He found that the F_2 generation was a mixed progeny of tall and dw for approxi-
mately three-f al F_3 genera-
tion. The ac tall and 277

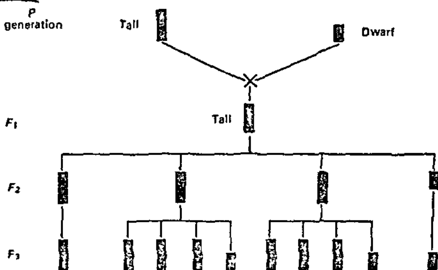


Fig 2.1. Diagram illustrating the inheritance of stem size in Mendel's experiment. The F_1 and succeeding generation were self-pollinated

dwarf plants In other words, the two original parental types (tall and dwarf) appeared in the F_2 generation in the approximate ratio of 3 : 1. This showed that dwarfness only disappeared in the F_1 generation but was not completely lost as it reappeared in the F_2 generation in 25% of plants. When the F_2 dwarfs were self-
warf offspring in the F_3 generation.
r, of two kinds. One-third (*i.e.*,
al F_2 progeny) on self-pollination

produced only tall plants in the F_3 and succeeding generations, and were, therefore, pure talls. The remaining two-thirds (*i.e.*, fifty per cent of the total F_2 plants), when self-pollinated (selfed), produced both talls and dwarfs in the ratio of 3 : 1 like the F_1 hybrids (Fig. 2.1) The F_2 generation thus consisted of three kinds of plants and not of two kinds as would appear from the outside. The three kinds of F_2 plants and the proportion in which they appear are given below.

1. Tall plants (about 25% of all the F_2 plants) which on self-pollination produced only tall plants—**pure talls.**

2 Tall plants (about 50% of all the F_2 plants and in

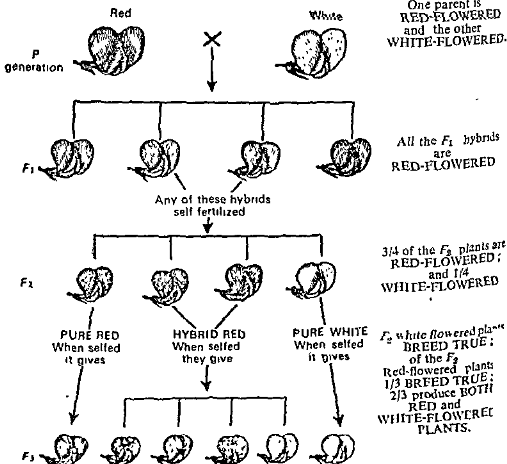


Fig. 2.2. Inheritance of flower colour in Mendel's experiment

appearance like the other talls) which, when self-pollinated, produced talls and dwarfs in the ratio of 3 : 1—**hybrid talls.**

3. Dwarf plants (about 25% of all the F_2 plants) which on self-pollination produced only dwarf plants—**pure dwarfs.**

The 3 : 1 ratio in the F_2 generation is, therefore, in reality a ratio of 1 pure tall : 2 hybrid talls : 1 dwarf. The above results are represented diagrammatically in figure 2.1.

Similar results were obtained by Mendel on the inheritance of other characters *e.g.*, red and white flowers, round and wrinkled seeds, yellow and green cotyledons, etc. For example, when a red-flowered variety was crossed with a white-flowered variety, the F_1 hybrids were all red-flowered. The F_1 hybrids on self-pollination gave rise to a mixed F_2 generation of red-flowered and white-flowered plants in the approximate ratio of 3 : 1. The white-flowered F_2 plants on self-pollination always produced white offspring in the succeeding generations but the F_2 red-flowered plants were of two kinds. One-third on self-pollination always produced red-flowered offspring in the F_3 and succeeding generations like the original red-flowered plants. The remaining two-thirds produced a mixed progeny of red-flowered and white-flowered plants in the ratio of 3 : 1 like the F_1 hybrids. These results are illustrated in figure 2.2.

DOMINANCE

Mendel gave some very good explanations for the observed results of his hybridisation experiments. Reverting to the cross between the tall and the dwarf varieties, we find that only the character of one parent a
the other remains hidden. I
of tallness is more potent and
dwarfness which is prevented
however, is not completely eli
in 25% offspring in the F_2 generation. In Mendelian terminology a character that shows itself in the hybrid is called **dominant** and the alternative one that fails to show itself is called **recessive**. Thus, tallness is dominant and dwarfness is recessive. Similarly, in the cross between the red-flowering and white-flowering varieties, the F_1 hybrids are red-flowering because red flower colour is dominant over white flower colour. This is **Mendel's conception of dominance,** which states that in crossings between organisms pure for contras-

ting characters of a pair, only one character of the pair appears in *the F_1 generation.*

Mendel studied, in all, seven differentiating traits in peas. These traits and the dominant in each case are given below :

	Trait studied	Dominant	Recessive
1.	Seed form	Round (R) (Smooth)	Wrinkled (r)
2.	Cotyledon colour	Yellow (Y)	Green (y)
3.	Seed coat colour	*Grey (G)*	*White (g)*
4.	Pod shape	*Inflated (I)*	*Constricted (i)*
5.	Pod colour	*Green (G)*	*Yellow (g)*
6.	Flower position	Axial (A)	Terminal (a)
7.	Stem length	*Tall (T)*	*Dwarf (t)*

importance. Let us illustrate this by an example from the inheritance of human beings There is a form of idiocy due to a recessive

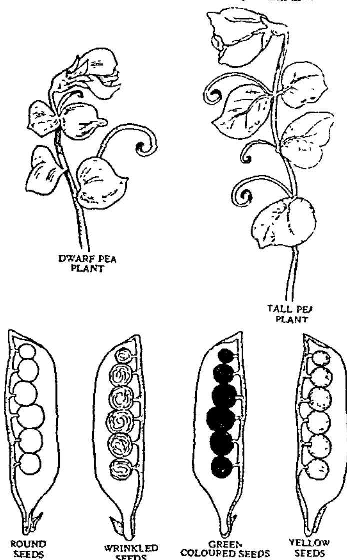


Fig. 2.3 Some of the contrasting characters in pea plant, studied by Mendel. The seed colour is due to cotyledons

gene. Let the dominant gene for normal be designated as N and its recessive allele for idiocy as n. A person who was hybrid for idiocy (Nn) would appear perfectly normal. If he married a normal woman (NN), all his children would be apparently normal because each would get a dominant gene for normal from the mother. But half of the children would on an average be hybrids

(*Nn*) as they would get the gene for idiocy from their father. If these hybrids in turn married pure normals, all the children again would be normal in appearance, though half on an average would be hybrids. Thus, the idiot gene might exist for several generations in hybrids without showing itself and the hybrid might look back over his family tree for many generations without finding an idiot ancestor. But if he married a hybrid woman of similar family history, he might have some idiot children, for both parents would now be hybrids ($Nn \times Nn$). They would produce children in the ratio of 3 normals : 1 idiot (*nn*). Thus, hybrid parents, neither of whom suspected idiocy in himself (herself) or his (her) ancestors, might have an idiot child of the hereditary type under discussion.

LAW OF SEGREGATION

Let us return to Mendel's experiment with the tall and dwarf pea plants The fact that some dwarf plants appeared in the F_2 generation clearly indicates that the factor for dwarfness was transmitted through the tall F_1 plants unaffected by its close association with the factor for tallness. It simply skipped a generation. Mendel explained the observed results in the F_2 generation by assuming that the two parental traits or their factors did not mix or fuse with each other in the F_1 hybrid but simply remained together without contaminating or diluting each other. When the F_1 hybrid forms gametes (or spores in plants), the factors of an allelomorphic pair separate or segregate from each other. A gamete (or spore) thus receives only one factor of a pair. In other words, while an [illegible] pair, a gamete individual can carry [illegible] can will carry only one [illegible] nete carry both factors of [illegible] not may carry the factor for tallness or for dwarfness but [illegible] carry both ; a factor for coloured flower or for white flower, but never both. This important deduction is known as the **law of segregation of characters** or **Mendel's first law of heredity**. It states that when a pair of alleles is brought together in hybrid union, the members of the allelic pair remain together without mixing and separate from each other when the hybrid forms gametes [illegible] to this law the F_1 hybrid tall peas of Mendel's [illegible] s of gametes, some carrying the [illegible] number carrying the factor for [illegible] dwarfness. As the gametes will be pure for tallness or for dwarfness,

the law is also known as the law of the purity of gametes—purity, that is, with reference to one member of an allelomorphic pair. Let us see how Mendel's law explains the observed numerical results of his experiments.

It will be evident that the original tall parent will have two genes for tallness *TT*, having received one from each of its two parents. Similarly, the dwarf parent will have two genes *tt* The gametes formed by the tall parent will each have a gene *T* and the gametes of the dwarf parent will have a factor *t* each. Their union will form an F_1 hybrid carrying the factors *Tt* This hybrid will be tall because *T* dominates over *t*. When the F_1 hybrid forms gametes, the two factors *T* and *t* separate from each other and the result is the formation of two kinds of gametes in equal numbers, half carrying the factor *T* and half carrying the factor *t*. This is in accordance with Mendel's law of segregation of characters. As a result, two kinds of pollen grains and two kinds of ovules are formed in the hybrid pea. The pollen-grain *T* has an equal chance of fertilizing an ovule *T* or *t*, producing seeds with *TT* or *Tt* combination. When the number of fertilizations is very large, as happens in nature, the two kinds of seeds produced by the *T* type of pollen-grains will be approximately equal. Similarly, the pollen grains of the *t* type have an equal chance of fertilizing the ovules *T* or *t*, producing *Tt* and *tt* seeds in equal number. The results to be expected on theoretical considerations are shown in figure 2.4. The F_2 generation will, therefore, consist of three kinds of plants in the following ratio :

1 Pure tall (*TT*) : 2 hybrid talls (*Tt*) : 1 dwarf (*tt*), or 3 talls 1 dwarf. This is shown diagrammatically in figure 2.4.

On the basis of this law Mendel had predicted that of the F_2 tall plants one-third will produce only talls and two-thirds will produce a mixed progeny of talls and dwarfs in the ratio of 3 : 1 in the F_3 generation. These results obtained from theoretical considerations on the assumption of segregation of characters are in complete accord with the numerical data obtained in actual experiments. No other explanation of the behaviour of hereditary traits through successive generations of hybrids has yet been given.

Mendel's laws have been found to hold good in the case of animals also. Thus, when a pure black guinea pig is mated with a white guinea pig, the animals produced in the F_1 generation are all black. They are hybrids. When any two hybrid black guinea

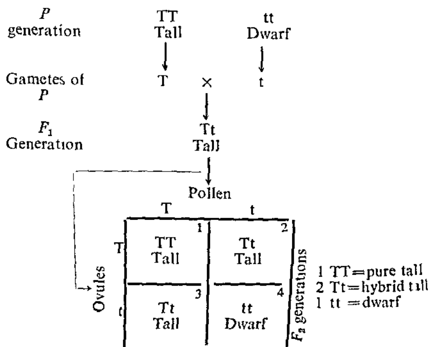


Fig. 2 4. Results of a cross between a tall and a dwarf pea plant upto the F_2 generation, giving the genotypes and phenotypes of parents, the gametes formed by them, and the genotypes and phenotypes of F_1 and F_2 plants

pigs are mated, the animals produced in the F_2 generation will be three blacks : 1 white. The blacks are of two kinds : one-third are pure black that breed true and two-thirds are again hybrids which when inbred produced a mixed progeny of blacks and whites in the ratio of 3 : 1. The results are shown in figure 2.5.

Mendel's law of segregation may be defined as *the non-mixing of alleles in the hybrids*. This is the most fundamental principle in all heredity. What it means is this that if a good

together in a hybrid they will not

other even *if they continue* to be

together in hybrids, generation after generation. They do not mix. A good gene is just as good when it leaves the hybrid as when it entered it and the bad allele is just as bad.

The 1 : 2 : 1 ratio is also obtained in the case of a cross between a pure red-flowering variety and a white-flowering variety of pea. The results of such a cross are shown diagrammatically in figure 2.2. Similar results were obtained by Mendel in crosses involving other pairs of contrasting characters in peas, for example round and wrinkled seedcoats, yellow and green cotyledons, etc.

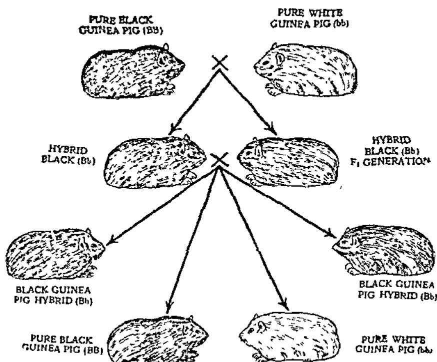


Fig. 2 5. Inheritance of coat colour in guinea pigs

Some of the numerical results actually obtained by Mendel are given in the table below :

TABLE 2.1.

Mendel's data of dominant traits in garden peas

Trait studied	Nos. in the F_2 generation		Ratio of dominants to recessives
	Dominant	Recessive	
Seed form	Round =5,474	Wrinkled =1,850	2 96 : 1
Cotyledon colour	Yellow =6,022	Green =2,001	3 01 : 1
Seed coat colour	Grey = 705	White = 224	3·15 : 1
Pod shape	Inflated = 882	Constricted = 299	2 95 : 1
Pod colour	Green = 428	Yellow = 152	2 82 : 1
Pod position	Axial = 651	Terminal = 207	3 14 : 1
Stem length	Tall = 787	Dwarf = 277	2·84 : 1
Total	Dominants=14,949	Recessives=5,010	2·98 : 1 or approximately 3 : 1

It will be noticed that in the case of each pair of characters, the difference in the actual and the expected ratios between the dominant and the recessive characters was no greater than might be expected when chance is the only factor. Mendel's experiments and his *numerical results calculated on the basis of the law of segregation* have been confirmed by numerous scientists working on other contrasting characters of a very great variety of plants and animals as given in the table below :

Organism	Dominant	Recessive	Appearance of F_1 hybrids	F_2 ratio
Guinea pig	Black coat	white	Black	3 : 1
Rabbit	"	"	"	3 : 1
Mice	Normal body size	dwarf	Normal	3 : 1
Man	Brown eye	blue	Brown	3 : 1
	Six fingers	five	Six	3 : 1
	Short stature	tall	Short	3 : 1
Tomato	Red fruit colour	yellow (flesh)	Red	3 1
	Yellow skin	transparent	Yellow	3 : 1
	Spherical fruit shape	oval	Spherical	3 : 1
	purple stem	green	Purple	3 : 1
Sorghum (Great millet)	Blackish purple colour of glume	brown	Blackish Purple	3 · 1
	pithy stalk	juicy stalk	Pithy	3 · 1
	Sweet stalk	non-sweet	Sweet	3 : 1
	Pink colour of grain	white	Pink	3 : 1
	Umbonate shape of grain	round	Umbonate	3 : 1
	Pearly grain	chalky grain	Pearly	3 : 1
	Awnless	awned	Awnless	3 : 1
Ragi (Finger millet)	Stigma fully feathered	stigma base feathered	Fully feathered	3 : 1
	Purple pigment in leaf (*PP*)	green (*pp*)	Purple	3 : 1
Maize	Coloured pericarp	colourless	Coloured	3 : 1
	Full endosperm	shrunken	Full	3 : 1
Rice	starchy endosperm	glutinous endosperm	Starchy	3 : 1
	Lax panicle	dense panicle	Lax	3 . 1
Bengal gram	Pink colour of petals	white	Pink	3 : 1
	Single flower to a branch	two flowers	Single	3 : 1
Chillies	Round shape	long	Round	3 : 1
	Pendant fruit	erect	Pendant	3 : 1
	Pungent fruit	non-pungent	Pungent	3 : 1

The inheritance of these and many other traits follows a definite pattern, which may be stated in general terms as under. If A stands for the constant dominant gene (or *factor*), and a for the constant recessive gene, then the hybrid from a cross between a pure dominant and a pure recessive parent must be Aa. In most cases, it resembles the dominant parent (*see* cases of incomplete dominance mentioned later). When the F_1 hybrids reproduce among themselves, the offspring in F_2 generation will be represented as under : $AA + 2Aa + 1aa$ or 1 pure dominant +2 hybrid dominants+1 recessive. The recessive disappears in the F_1 generation but is not completely lost. In spite of its close association with the dominant in the F_1 generation it reappears unaffected in 25% of the F_2 progeny.

Proof of segregation. There are two strains of rice, one in which the endosperm has starchy grains and the other in which the endosperm has glutinous grains. Starchy grains stain deep blue with iodine and the other type stain reddish to dark-brown. Their pollen grains give the same iodine reaction as the endosperm. The F_1 offspring of a cross between these two varieties received a gene from each of the parents and were hybrids When the pollen of the [illegible]

other words, there was segregation of factors in the pollen grains.

The test cross. Mendel's law of segregation, often called Mendel's first law of heredity, can be checked by the backcross method. If a hybrid F_1 is backcrossed to the pure recessive parent, then the law of segregation should give a 1 : 1 ratio in the progeny. The F_1 tall hybrid (Tt) would form gametes T and t; and the gametes of the dwarf parent will be all t. Chance unions between these should give 50% Tt and 50% tt, or a 1 : 1 ratio of tall and dwarf as shown in the lower row of figure 2.4.

The results obtained in actual experiment agree completely with theoretical expectations. Tl [illegible] is also called the test cros[illegible] portion of different kinds of [illegible]

Phenotype and genotype. [illegible] of tall and dwarf peas, we find that the talls are of two kinds. One-third of them are TT and two-thirds Tt. Both types have the same external appearance but differ in their genetic behaviour.

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	Spherical fruit shape	oval	Spherical	3 · 1
	purple stem	green	Purple	3 : 1
Sorghum (Great millet)	Blackish purple colour of glume	brown	Blackish Purple	3 . 1
	pithy stalk	juicy stalk	Pithy	3 : 1
	Sweet stalk	non-sweet	Sweet	3 : 1
	Pink colour of grain	white	Pink	3 : 1
	Umbonate shape of grain	round	Umbonate	3 : 1
	Pearly grain	chalky grain	Pearly	3 : 1
	Awnless	awned	Awnless	3 : 1
Ragi (Finger millet)	Stigma fully feathered	stigma base feathered	Fully feathered	3 : 1
	Purple pigment in leaf (*PP*)	green (*pp*)	Purple	3 : 1
Maize	Coloured pericarp	colourless	Coloured	3 : 1
	Full endosperm	shrunken	Full	3 : 1
Rice	starchy endosperm	glutinous endosperm	Starchy	3 : 1
	Lax panicle	dense panicle	Lax	3 : 1
Bengal gram	Pink colour of petals	white	Pink	3 : 1
	Single flower to a branch	two flowers	Single	3 : 1
Chillies	Round shape	long	Round	3 : 1
	Pendant fruit	erect	Pendant	3 : 1
	Pungent fruit	non-pungent	Pungent	3 : 1

The inheritance of these and many other traits follows a definite pattern, which may be stated in general terms as under. If A stands for the constant dominant gene (or *factor*), and a for the constant recessive gene, then the hybrid from a cross between a pure dominant and a pure recessive parent must be Aa. In most cases, it resembles the dominant parent (*see* cases of incomplete dominance mentioned later). When the F_1 hybrids reproduce among themselves, the offspring in F_2 generation will be represented as under : $AA + 2Aa + 1aa$ or 1 pure dominant +2 hybrid dominants+1 recessive. The recessive disappears in the F_1 generation but is not completely lost. In spite of its close association with the dominant in the F_1 generation it reappears unaffected in 25% of the F_2 progeny.

Proof of segregation There are two strains of rice, one in which the endosperm has starchy grains and the other in which the endosperm has glutinous grains. Starchy grains stain deep blue with iodine and the other type stain reddish to dark-brown. Their pollen grains give the same iodine reaction as the endosperm. The F_1 offspring of a cross between these two varieties received a gene from each of the parents and were hybrids. When the pollen of the F_1 hybrids was treated with iodine 50% of the pollen grains stained d[illegible] th[illegible] a[illegible] other words, there was segregation of factors in the pollen grains.

The test cross. Mendel's law of segregation, often called Mendel's first law of heredity, can be checked by the backcross method. If a hybrid F_1 is backcrossed to the pure recessive parent, then the law of segregation should give a 1 : 1 ratio in the progeny. The F_1 tall hybrid (Tt) would form gametes T and t; and the gametes of the dwarf parent will be all t. Chance unions between these should give 50% Tt and 50% tt, or a 1 : 1 ratio of tall and dwarf as shown in the lower row of figure 2.4.

The results obtained in actual experiment agree completely with theoretical expectations. The backcross with the recessive parent is also called the test cross because it is a direct test of the propo[illegible] by the F_1 hybrid.

[illegible] to the F_2 generation of [illegible] alls are of two kinds. One-third of them are TT and two-thirds Tt. Both types have the same external appearance but differ in their genetic behav

Such external similarities and differences in inheritance are expressed by the use of two terms, namely phenotype, and genotype, first employed by Johanssen in 1911. Phenotype refers to the external appearance of an organism regardless of its genetic make-up and genotype refers to its genetic composition or hereditary constitution irrespective of its external appearance. The *TT* and *Tt* talls have the same phenotype but belong to different genotypes Thus, the same phenotype may be produced by different genotypes Likewise, one genotype may produce different phenotypes because of the effect of different environments. Thus, a plant with genes for green colour will develop green colour in the leaves in the presence of light and another plant with the same genotype will not develop the green colour if light is cut off. Similarly, a plant with genes for tallness may remain dwarf on account of poor nutrition. An organism in which the two genes for a trait are identical is said to be pure, or **homozygous for this particular trait**. When the two alleles for a trait, received from the parents, are different, the organism is said to be **hybrid or heterozygous for this trait**. Thus, pea plants with *TT* and *tt* are homozygous, the former for tallness and the latter for dwarfness. The plants *Tt* are heterozygous for stem length. The homozygous individuals produce only one kind of gametes and those that are heterozygous for one trait produce two kinds of gametes in equal numbers. In the case of the dominant traits both the homozygotes and heterozygotes have the same phenotype but the recessive trait is shown only in homozygous condition. From the above considerations it will be clear that the 3 : 1 ratio observed in the F_2 generation of hybrids is a phenotype ratio and the genotype ratio of the F_2 offspring is 1 : 2 : 1.

The homozygotes produce gametes of only one type. Such organisms when self-pollinated or crossed among themselves (*i.e.*, inbred) produce offspring all of which are like the parents both in their phenotype and genotype. In other words, the homozygous individuals breed true. The heterozygotes, on the other hand, produce two types of gametes in equal numbers and, when inbred, produce a mixed progeny, some showing the dominant trait and others, the recessive trait. In other words, they do not breed true. In most cases, the genotype of an individual cannot be determined from the phenotype. Such determinations must be made by breeding experiments as explained above or by back-crossing it with indivi-

duals showing the pure recessive trait. A homozygous dominant will produce, as a result of such a cross, offspring all of which show the dominant trait. In the case of heterozygous dominant the result will be a mixed generation, some showing the dominant phenotype and an equal number showing the recessive phenotype (*see* figure 2.4).

In our discussion so far, we have considered crosses involving only one pair of factors. Such crosses are called **monohybrid crosses**. In the case of a monohybrid cross, the phenotype ratio of 3 : 1 obtained in the F_2 generation is called the **monohybrid ratio.**

BREEDING MATERIAL

Genetic experiments will give accurate results if the number of offspring from a single mating is large and quite often experiments have to be carried out for many generations to see what happens from one generation to the next. Plants are the most suitable material for this purpose because most plants reproduce in a year or less and a single plant produces numerous seeds. Again, most plants are bisexual. To find out the result of selfing the F_1 hybrids all that is needed is to simply self-pollinate plants as Mendel did.

In the case of animals we have to choose those that mature early and produce many offspring at a time. Mice, rabbits, guinea pigs and insects are the most suitable. The study of heredity in man is a difficult problem because man is too slow a breeder to permit generalisations and does not submit to experimentation. [illegible] of genetics [illegible] to

GENETIC RATIOS

All genetic ratios are probability ratios. Thus, if two heterozygous black rabbits (Bb) are bred and produce exactly four offspring it is probable that three will be black and one white. But it might turn out that all might be black or all might be white. The latter possibility would rarely occur or the combination [illegible] black : 1 white; 2 black : 2 white or 1 black : 3 [illegible] occur. If a hundred such matings were made, however, [illegible] will be approximately 75 black : 25 white. [illegible]

white approaches more and more closely to 3 : 1 as large numbers of offspring are produced. The 3 : 1 ratio is an average ratio based on large numbers of offspring. The same is true of other ratios which will be described later on. This probability ratio can be stated in another way. In mating two heterozygous individuals (Bb) there are three chances out of four that any particular offspring will show the dominant character, and one chance out of four that it will show the recessive character.

In man brown eye colour is dominant over blue. If two heterozygous brown-eyed people mate, there are three chances out of four that their child will have brown eyes, and one chance out of four that it will have blue eyes. Each mating is a separate independent event. Thus, if two heterozygous brown-eyed parents have three brown-eyed children and are expecting a fourth child, the fourth one, too, has three chances out of four of being brown-eyed, and only one chance out of four of having blue eyes. It is also possible that every time the one chance out of four of producing a blue-eyed child might materialise in which case all the children will have the recessive blue-coloured eyes. This is what actually happened to a friend of the author. He and his wife were both heterozygous for brown eye colour. They had three children, all of them blue-eyed.

It must be remembered that the 3 : 1 and other ratios to be described in later pages are approximate ratios. Thus, in one of his experiments Mendel obtained in the F_2 generation 6,022 yellow and 2,001 green seeds. This gives an approximate but not an exact ratio of 3 . 1 In working out all genetical problems it is necessary to convert the numbers into approximate whole ratios

QUESTIONS

1. Which provide better material for the study of heredity? Plants or animals?
2. Quite often individual plants which resemble each other very closely behave very differently in breeding experiments Explain why?
3. The F_1 hybrids between two parents homozygous for a pair of contrasting characters are uniform in their appearance. Explain why.
4. Which is more important? The principle of segregation or the principle of dominance.

Note. In tomatoes red fruit colour (R) is dominant over yellow (r)

5. What kind of gametes as to fruit colour will be formed by the following plants? *RR, Rr, rr.*
6. A pure red fruited plant is crossed to a yellow fruited one? What will be the appearance of the F_1? The F_1 are interbred and produce 320 offspring in the F_2. How many of them will be red and how many yellow? What will be the genotypes of the F_2 and in what numbers?

7. The F_1 in question No 6 is crossed back to the red parent, to yellow parent. What will be the appearance of the offspring in each case ?
8. Give the genotypes, phenotypes and their properties of the offspring derived from the following crosses in tomatoes :
$RR \times rr$; $Rr \times rr$, $Rr \times Rr$; $rr \times rr$; $Rr \times RR$
9. A red fruited tomato plant is crossed to a yellow fruited one and produce 173 offspring 84 of them were red and 89 yellow. Determine the genotypes of the parents.
10. If the red-fruited parent in Q. No. 9 is self-fertilized, what kind of offspring will it produce as regards fruit colour ?
11. A cross between two red-fruit tomatoes produced 71 red and 23 yellow offspring. What are the genotypes of the parents ? What will each produce when crossed to a yellow-fruited plant ?
12. Suppose a pure red-fruited plant is crossed to a yellow variety, the F_1 self-fertilized, and counted 400 offspring in the F_2 Is it necessary that 300 of these be red and 100 yellow ? Give reason for your answer
13. In man brown eye (B) is dominant over blue (b). A man and his wife, both brown eyed, beget a blue-eyed child. What are the genotypes of the parents ?
14. The offspring of the above union (man) marries a brown-eyed woman who had a brown-eyed father, and a blue-eyed mother, and a blue-eyed brother. The man and woman have a brown-eyed child. Give the genotypes of (1) the parents of man and woman, (2) the man and woman, (3) their child.
15. A blue-eyed man marries a brown-eyed woman whose mother had blue eyes What proportion of the children would be expected to have blue eyes ?
16. In the Wyandottes breed of chickens rose comb (R) is dominant over single (r). How can we determine whether a particular rose comb bird is homozygous or heterozygous ?

3

MENDEL'S LAWS OF HEREDITY *(Contd.)*

LAW OF INDEPENDENT ASSORTMENT

LET us now co [illegible] which a cross is made [illegible] Such a cross [illegible] ganism which [illegible] selected for one [illegible] produced on self-pollination yellow round (smooth) seeds and the other, green wrinkled seeds. He crossed these varieties. In such a cross, the nature of F_1 generation could be judged without planting the seeds, for the characters involved, are really characters of the seeds and not of the mature grown up plants which, like stem length or flower colour, could be judged only after the seeds had germinated and developed into mature plants. *All the F_1 seeds from the cross were yellow round. Mendel knew from his experiments on monohybrid crosses that yellow colour and round form of* the seed were dominant over green and *wrinkled characters of the* seeds. It was immaterial which of the parents provided the pollen and which acted as the seed-bearing parent. In other words, reciprocal crosses gave the same result. When a cross was made between a variety which was pure for yellow wrinkled seeds with one having green round seeds, the result was the same, *i.e.*, the F_1 seeds were all yellow round. *They always* showed both dominant traits. It made no difference whether both dominants had originally been *in one parent*, or whether each of the parents had contributed one *of the dominant traits.* Furthermore, when the F_1 hybrids were

self-pollinated or crossed among themselves, the F_2 generation was also the same in either case. The results are shown diagrammatically in figure 3.1.

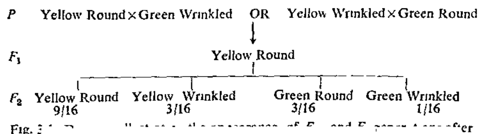


Fig. [illegible]

It will be seen that in the F_2 generation there appeared 4 kinds of offspring. Two of them showed the same combinations of characters as the parents but two of them were new combinations. The four kinds of plants, moreover, were not equally numerous but appeared in the definite ratio of 9 : 3 : 3 : 1. The actual count of the different kinds of F_2 seeds in one of Mendel's experiments is as under :

	Yellow round	Yellow wrinkled	Green round	Green wrinkled	Total
	315	101	108	32	556
OR	9·1/16	2·9/16	3·1/16	0·9/16	
OR Approximately	9/16	3/16	3/16	1/16	

The 9 : 3 : 3 : 1 ratio in the F_2 generation of a dihybrid cross is known as the dihybrid ratio. Mendel found the same ratio in the case of other characters in peas. Thus, in the case of a cross between a tall variety of peas which bore red flowers and a dwarf variety which bore white flowers, the appearances of the offspring in the F_1 and F_2 generations were as under :

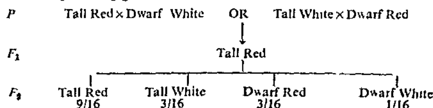


Fig. 3.2 Result of a cross between a tall pea plant which bears red flowers and a dwarf plant which bears white flowers

This ratio has been confirmed by several other workers in the case of a great variety of plants and animals, for dihybrid crosses involving independent characters which show complete dominance. Thus, in squashes white fruit colour is dominant over

yellow and "disc" shape of the fruit is dominant over sphere. A cross between white disc and yellow sphere varieties gives an F_1 generation of white disc plants. These, when crossed among themselves, produce an F_2 generation of white disc, white sphere, yellow disc, and yellow sphere types in the ratio of 9 : 3 : 3 : 1, as shown in figure 3.3.

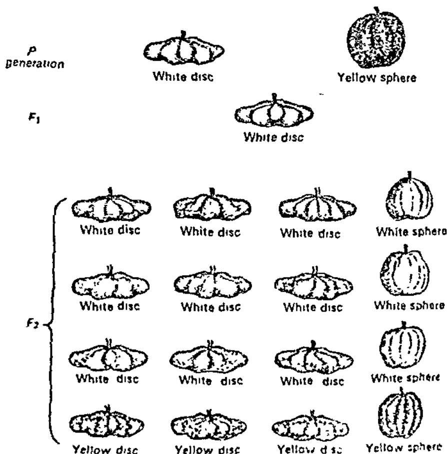


Fig. 3.3. The appearance of F_1 and F_2 generations in a double cross in squash. One of the parents has white disc fruits and the other, yellow sphere. White is dominant over yellow and disc shape over sphere. In the F_2 generation, there are 9/16 white, disc ; 3/16 white, sphere ; 3/16 yellow, disc ; and 1/16 yellow, sphere

The results obtained by Mendel led him to the discovery of the second major principle of inheritance, namely that **each pair of different characters in hybrid union is inherited independently of the other differences in the two original parental stocks.** *In other*

words, different characters or their genes behave as if they are independent of each other. In short, the different alleles of the same gene do not fuse but segregate in heterozygotes, and different gene pairs segregate independently of one another. This [illegible] tment [illegible] ndel's second law of inheritance. In the above example of peas, it will be noticed that seed colour is in no way tied to seed shape ; rather the two characters are inherited independently of each other. This is evident from the fact that in the F_2 generation, every possible combination of characters appears—yellow round, yellow wrinkled, green round, and green wrinkled. Further evidence in this matter is derived from the fact that it makes no difference to the results obtained in the F_2 generation whether both dominants were brought in by one parent and both recessives by the other, or whether each of the parents had contributed one of the dominants and one of the recessive (*see* page 24-25). The result was always the same. The F_1 shows both dominants and the F_2 offspring appear in the ratio of 9 double dominants : 3 with one dominant and one recessive : 3 with the other dominant and the other recessive : 1 double recessive.

The ratio of the four kinds of offspring in the F_2 generation is admirably explained by the principle of independent assortment. Let us first consider the two characters of seed colour and seed shape separately. Of the total F_2 plants 416 are yellow-seeded, and 140 green-seeded giving a ratio of 3 : 1 ; 423 are round-seeded and 133 are wrinkled-seeded, again giving an approximate ratio of 3 : 1. This 3 : 1 ratio in either case is explained on the basis of the law of segregation. Considering the two character pairs together, there are two possibilities. When the F_1 hybrids form gametes, either the seed colour will remain tied to the seed form in the same combinations in which it came from the parents or the two character pairs segregate independently of one another. Mendel showed that the latter possibility is realised. Yellow seeds number 3/4ths of the total F_2 progeny. Of these 3/4ths yellows, 3/4ths will be rounded and 1/4th wrinkled. This means that yellow-round seeds will be 9/16th ($3/4 \times 3/4$) and yellow wrinkled will be 3/16ths ($1/4 \times 3/4$) of the total F_2 progeny. Similarly, of the 1/4th green seeds, 3/4ths will be round and 1/4th will be wrinkled giving a total of 3/16ths ($3/4 \times 1/4$) green round and 1/16 green wrinkled seeds ($1/4 \times 1/4$) of the entire progeny.

A simple method for deriving the phenotypic combinations of a dihybrid cross is the forkedline method illustrated in figure 3.4. The monohybrid ratio is first worked out separately for each character pair. In cases showing dominance it will be 3 : 1. The 3 : 1 ratio for one monohybrid cross is then combined with the 3 : 1 ratio for the other monohybrid cross as in figure 3.4.

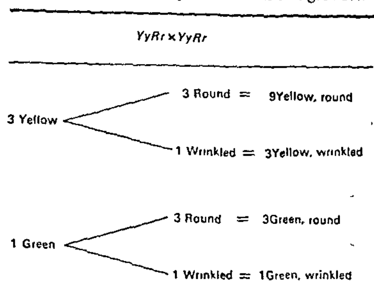


Fig. 3.4. Deriving the phenotypes of the progeny (F_2) of a cross between identical dihybrids (*Rr*) *y*×*RrYy* in this case)

The above explanation will be better understood if the characters or their genes are represented by letters. Let *R* (dominant), and *r* (recessive) stand for the round and wrinkled seed shape respectively ; *Y* (dominant) and *y* (recessive) for the yellow and green seed colour. The original parents used in Mendel's cross would have the genotype *YYRR* (yellow, round seed) and *yyrr* (green wrinkled) The gametes of *YYRR* parent would all be *YR* and those of the other parent *yr*. F_1 offspring resulting from the union of these gametes would be a double heterozygote *YyRr*. Now the essential point is this : what are the kinds of gametes formed by the F_1 hybrid ? The allelic pairs *Y-y* and *R-r* segregate independently of each other during the formation of gametes in the F_1 hybrids. Of each allelic pair a gamete can carry only one gene. Thus a gamete would carry *Y* or *y* and *R* or *r*. A gamete that carries *Y* must also contain a gene for seed form. [illegible] *Y* will be associated with *R* or *r* is a matter depending [illegible] chance. There is equal chance for *Y* [illegible] associated [illegible] with *r*. The [illegible]

gametes would, therefore, be of two kinds viz., *YR* and *Yr* in equal numbers. Similarly, the gametes carrying *y* would be of two kinds : *yR* and *yr* in equal numbers. There would in all be four kinds of gametes viz., *YR*, *Yr*, *yR* and *yr* in approximately equal numbers. Thus, a recombination of genes takes place at the time when the F_1 hybrid forms gametes The particular combination in which the genes entered the F hybrid from each original parent has no effect

therefore, independent of the pre-

random. This is the principle of independent assortment (recombination) or Mendel's second law of inheritance.

A simple and direct method for determining the various kinds of gametes formed by a dihybrid is the forked-line method. Gametes are first derived separately for each monohybrid. These are then combined with each other as illustrated in figure 3.5.

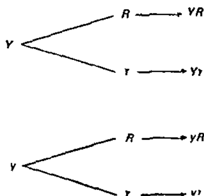


Fig 3.5. Genotypes of gametes formed by dihybrid *YyRr*, undergoing independent segregation

The various kinds of genotypes to be expected in the F_2 generation of a dihybrid cross may be determined by one of the following two methods :—

1. **Punnet's checkerboard method**. The F_1 dihybrids, as we have seen above, form four kinds of pollen-grains and four kinds of ovules in equal numbers with the gene combinations *YR*, *Yr*, *yR* and *yr*. Union of these gametes is a random process, the four types of pollen-grains having equal chance of effecting fertilization ; and the four types of ovules having equal chance of being fertilized. Which type of ovule a particular kind of pollen-grain will fertilize is purely a matter of chance. There being four kinds of pollen-grains and four kinds of ovules, the number of possible combinations between them in the F_2 generation will be sixteen (4×4). It should be noted that the number of combinations which can appear in the gametes or from their union is limited only by the number of combinations mathematically possible. As any combination is as likely to be effected as any other, the sixteen possible combinations will be equally numerous.

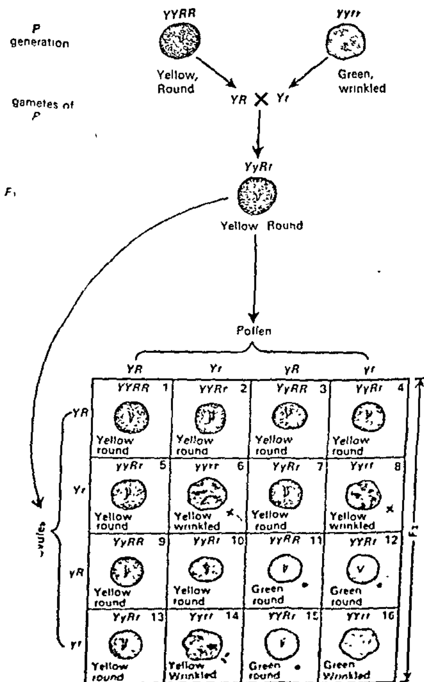


Fig. 3.6. Mendel's law of independent assortment. Diagram showing the phenotypes and genotypes of parents, F_1 plants and their gametes, and F_2 plants when a pea plant which is pure for yellow round seeds is crossed with a pea plant which bears green wrinkled seeds.

Now make a checkerboard with 16 squares, four horizontal rows corresponding to the gametes of one sex, and four vertical rows corresponding to the gametes of other sex. The four types of pollen are written in a horizontal row above the checkerboard, a different type being written outside each of the four squares in the row. Similarly, write the four types of ovules in a vertical row on the left of the checkerboard (Fig. 3.6). Fill in the 16 squares by multiplying the genotypes of the pollen and ovules. The 16 squares represent the 16 possible combinations of gametes which might result in the zygotes. The phenotypes of the zygotes can be read by applying the law of dominance By learning the method of making the checkerboard one can easily foretell the possible results of any mating.

The genotypes and the phenotypes of the F_2 offspring of the dihybrid cross discussed above are shown in the sixteen squares of the checkerboard in figure 3.6. The squares have been serially numbered for convenience. A count of these squares shows that the F_2 generation consists of four phenotypes as under :

Phenotypes	Square numbers	Total
Yellow round	1, 2, 3, 4, 5, 7, 9, 10, 13	9
Yellow wrinkled	6, 8, 14	3
Green round	11, 12, 15	3
Green wrinkled	16	1

2. **Forked-line method.** The dihybrid is treated as consisting of two monohybrid crosses. The genotypes of the zygotes are first determined for each of the two monohybrid crosses. They are then combined by the forked-line method in the manner explained earlier for deriving the genotypes of gametes. In the example being considered the genotypic ratio of 1 : 2 : 1 is expected for each monohybrid cross. The two monohybrid ratios are then combined as shown in figure 3.7. The phenotypes of the resulting zygotes are read from the genotypes as usual.

Both the methods described above give the theoretical ratio of 9 yellow round : 3 yellow wrinkled : 3 green round : 1 green wrinkled. The ratio is to be found only when both characters show complete dominance. Each character is inherited independently of every other character, or behaves as a separate unit. The principle of independent assortment is also known as the principle of unit characters. The Mendelian theory of unit characters completely accounts for the numerical data obtained in actual experiment. No other theory has yet been suggested which

can account for it. In fact, 9 : 3 : 3 : 1 ratio could be predicted on the basis of *Mendel's second law.*

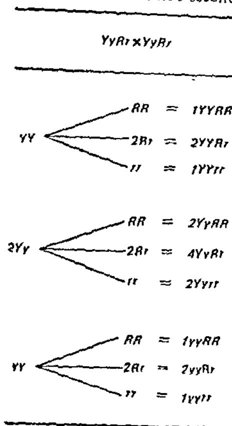


Fig. 3.7. The genotypes of the F_2 generation resulting from the self-pollination of a dihybrid garden pea of the genotype YyRr. The results are the same as obtained by the checkerboard method

The 9 : 3 : 3 : 1 ratio which is obtained in *F_2 generation of a* cross involving two allelic pairs is called the **dihybrid ratio.** This ratio is a phenotype ratio. The *offspring belonging to the four* phenotypes fall under nine different genotypes. Out of the sixteen possible combi*nations shown in figure 3.6,* only four are homozygous for both characters ; the others are heterozygotes of different degrees. The homozygotes *lie* in the diagonal row of squares running from the upper left to the lower right corner of the checkerboard. These four be*long to different phenotypes* and will breed true. They represent all the possibilities as regards true breeding forms to *be expected from the dihybrid* cross. The others are all *hetero*zygotes and on self-breeding show different degrees of segregation. The *numerical* count of the different phenotypes and genotypes to be expected in the F_2 generation from the above dihybrid cross are summarised in *tabular form in table 3.1.*

It will be noticed that while there are four phenotypes in the F_2 generation, the number of genotypes is 9. Similar results are obtained in crosses involving *other character pairs. For example,* in a cross between a tall pea plant bearing coloured flowers and a dwarf plant bearing white flowers, the F_1 hybrids are all tall and bear coloured flowers, because tall stem is dominant over *dwarf stem and the character of coloured flowers is dominant over white*

TABLE 3.1. Summarised result (F_2) of figures 3.6 and 3.7 relating to a cross between a pea variety with yellow round seeds and one with green wrinkled seeds

Phenotypes	Genotype	Genotypic frequency (with sq. Nos in which they lie)	Phenotypic ratio	Breeding behaviour on self-fertilization
Yellow, round	YYRR	1 (sq. 1)	9	Breeds true for both traits
	YYRr	2 (sq. 2, 5)		Breed true for yellow colour only
	YyRR	2 (sq. 3, 9)		Breed true for round seed only
	YyRr	4 (sq. 4, 7, 10, 13)		Segregate for both traits
Yellow, wrinkled	YYrr	1 (sq. 6)	3	Breeds true for both traits
	Yyrr	2 (sq. 8, 14)		Breed true for wrinkled seeds only
Green, round	yyRR	1 (sq. 11)	3	Breeds true for both traits
	yyRr	2 (sq. 12, 15)		Breed true for green colour only
Green, wrinkled	yyrr	1 (sq. 16)	1	Breeds true for both traits.

flowers. The F_2 generation obtained from the self-pollination of the F_1 plants consists of four kinds of plants (phenotypes), tall coloured, tall white, dwarf coloured and dwarf white in the approximate ratio of 9 : 3 : 3 : 1. It was immaterial whether the tall coloured plant provided the pollen and the dwarf white plant acted as the seed-bearing parent or *vice versa*. Similarly, the same results were obtained if a tall white plant was crossed with a dwarf one bearing coloured flowers. In other words, the character of stem length was in no way tied to that of flower colour. The two characters assorted independently in inheritance. The results are shown diagrammatically in figure 3.8.

The test cross of the dihybrid. Mendel's law of independent assortment can be checked by crossing back the F_1 hybrid with

the double recessive parent. The plants grown from the F_2 yellow round seeds have the genotype *YyRr*, and will form four kinds of

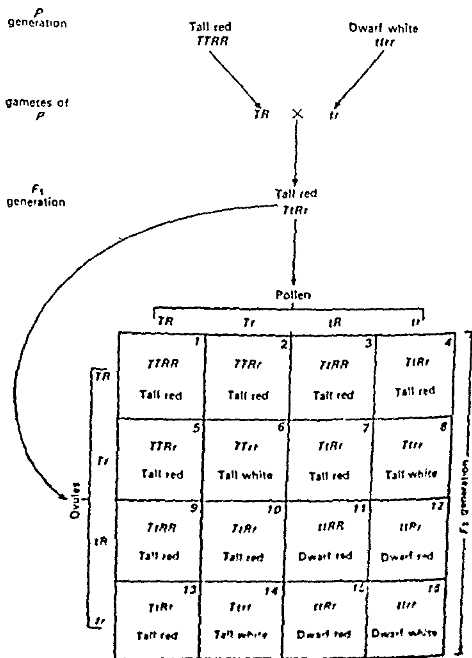


Fig. 3.5 Result of a dihybrid cross between a pea plant which is pure for tall stem and bears red flowers, and a pea plant which is dwarf and bears white flowers. The F_1 plants were self pollinated.

gametes in approximately equal numbers. These are *YR*, *yR*, *Yr* and *yr*. The double recessive parent with green wrinkled seeds has the constitution *yyrr* and will produce gametes of only one kind, viz., *yr*. A cross between the two should result in four possible

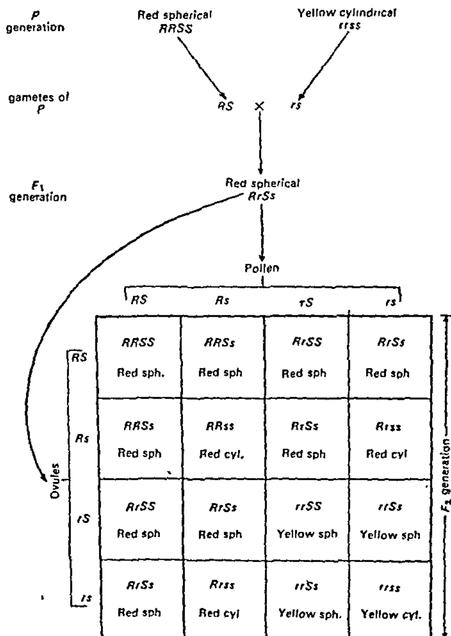


Fig. 3.9. Result of a cross between a tomato plant which is pure for red flesh and spherical fruit, and a tomato plant which has yellow cylindrical fruits

combinations in approximately equal numbers as shown in the lowermost row of squares in figure 3.6. The expected *ratio of seeds* would be 1 yellow round : 1 green round : 1 yellow wrinkled : 1 green wrinkled. The actual numbers obtained in one of Mendel's experiments were 55 yellow round, 51 green round, 49 yellow wrinkled, and 52 green wrinkled. The results obtained in actual experiments conform to the theoretical expectation, thus confirming Mendel's second law.

Let us examine a few cases of dihybrid crosses in the crop plants. In tomatoes red flesh (*R*) of fruit is dominant over yellow flesh (*r*) spherical fruit shape (*S*) over oval or cylindrical shape (*s*) and yellow skin (*Y*) over transparent skin (*y*). In the cross, pure red flesh and spherical shape (*RRSS*) × pure yellow flesh and cylindrical fruit shape (*rrss*) or pure red flesh and cylindrical shape (*RRss*) × pure yellow flesh and spherical shape (*rrSS*) the F_1 hybrids are uniformly red flesh and spherical shape (*RrSs*). The hybrids when inbred give an F_2 progeny of 9 red spherical : 3 red cylindrical : 3 yellow spherical : 1 yellow cylindrical as shown in figure 3.9. The back-cross between the F_1 and the double recessive parent (*rrss*) gives a ratio of 1 red spherical : red cylindrical : 1 yellow spherical : 1 yellow cylindrical as given below:

Gametes of F_1 hybrid (*RrSs*)

		RS	Rs	rS	rs
Gametes of double recessive parent rrss	rs	RrSs Red spherical	Rrss Red cylindrical	rrSs Yellow spherical	rrss Yellow cylindrical

Similarly in the cross red flesh, yellow skin (*RRYY*) × yellow flesh, transparent skin (*rryy*) the F_1 hybrids are red flesh, yellow skin (*RrYy*) and the F_2 gives a ratio of *9* bright red : 3 *dull* red : 3 deep golden yellow : 1 pale yellow as shown in the checkerboard on page 37.

In sorghum (great millet), umbonate shape (*U*) of grain is dominant over round (*u*), and pink colour (*W*) of grain is *dominant* over white (*w*). The two character pairs are inherited independently of each other. The F_1 hybrids of umbonate, pink (*UUWW*) × *round*, white (*uuww*) are the double heterozygotes umbonate, pink (*UuWw*).

The F_2 progeny consists of umbonate pinks, umbonate whites, round pinks and round whites, in the ratio 9 : 3 : 3 1. The test cross between F_1 dihybrids (*UuVv*) and the double recessive parent (*uuvv*) gives the four types of phenotypes in the ratio of 1 : 1 : 1 : 1. Let the studsnts make the checkerboard themselves and derive these ratios.

$F_1 = RrYy$

Pollen

Ovules

	RY	Ry	rY	ry
RY	RRYY Bright red	RRYy Bright red	RrYY Bright red	RrYy Bright red
Ry	RRYy Bright red	RRyy Dull red	RrYy Bright red	Rryy Dull red
rY	RrYY Bright red	RrYy Bright red	rrYY Golden yellow	rrYy Golden yellow
ry	RrYy Bright red	Rryy Dull red	rrYy Golden yellow	rryy Pale yellow

TRIHYBRID AND POLYHYBRID RATIOS

Crosses involving three or more pairs of alternative characters that are inherited independently are called trihybrid and polyhybrid crosses. The F_1 hybrids of such crosses are called trihybrids and polyhybrids. If all the characters show complete dominance, the trihybrids and polyhybrids will show all the dominant characters. Thus, when a pea plant which is pure for yellow and round seeds and also for tall stem is crossed with one having green

wrinkled seeds and dwarf stem the F_1 will be a trihybrid (*YyRrTt*) and its phenotype will be yellow round and tall. It will form eight kinds of gametes. The checkerboard method can be employed for working out the phenotypic and genotypic ratio in the F_2 generation but this will require a large checkerboard with 64 squares which is not convenient. In trihybrid and polyhybrid crosses, therefore, the forked line method is often preferred.

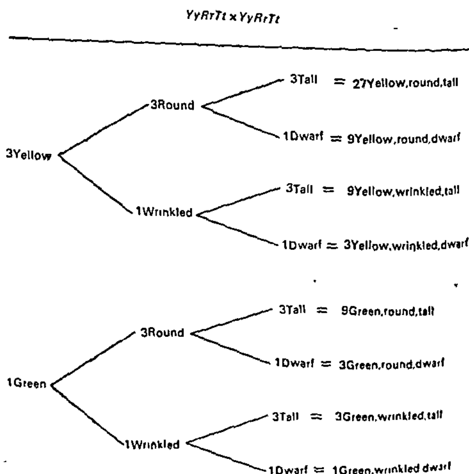


Fig. 3.10. Phenotypes of the F_2 generation of a trihybrid cross between a variety of garden peas with yellow, round seeds and tall stem, and a variety which has green, wrinkled seeds and dwarf stem, as derived by the forked-line method. The figure represents the phenotypic result of self-pollination of a trihybrid with the genotype *YyRrTt*

The ratios are first worked out for each character pair separately. These are then combined with one another in the manner illustrated for the above example in figure 3.10.

The F_2 phenotypic ratio in the example of the trihybrid cross comes to 27 : 9 : 9 : 3 : 9 : 3 : 3 : 1. Quite often in genetic problems it is necessary to determine the genotypes of gametes formed by a trihybrid and to work out both the phenotypic and genotypic trihybrid ratios. The genotypes of different kinds of gametes formed by a trihybrid (and polyhybrid) are arrived at by the forked-line method. First the gametes are derived for one allelic pair, then for the second pair, then for the third pair and so on. They are then combined as shown in figure 3.11. The trihybrid genotype ratio in the F_2 may be worked out by the forked-line method.

The genotypic ratio is first worked out separately for each

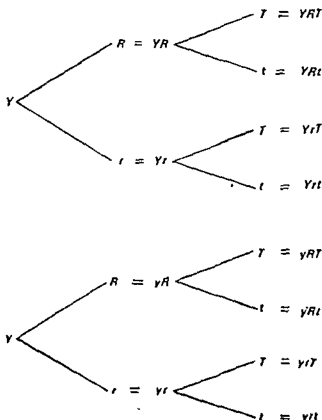
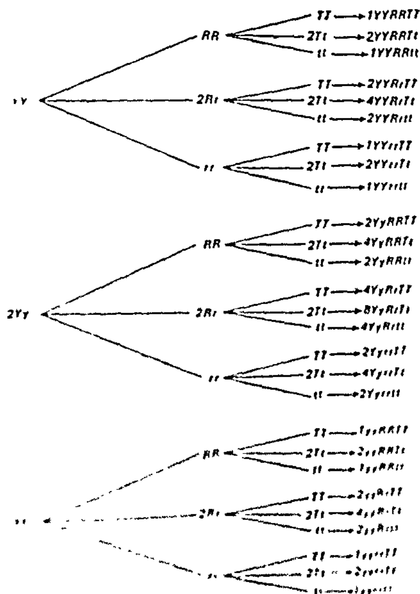


Fig. 3.11. Genotypes of the gametes formed by the trihybrid *YyRrTt*


YyRrTt x YyRrTt
YY
RR
TT → 1YYRRTT
2Tt → 2YYRRTt
tt → 1YYRRtt
2Rr
TT → 2YYRrTT
2Tt → 4YYRrTt
tt → 2YYRrtt
rr
TT → 1YYrrTT
2Tt → 2YYrrTt
tt → 1YYrrtt
2Yy
RR
TT → 2YyRRTT
2Tt → 4YyRRTt
tt → 2YyRRtt
2Rr
TT → 4YyRrTT
2Tt → 8YyRrTt
tt → 4YyRrtt
rr
TT → 2YyrrTT
2Tt → 4YyrrTt
tt → 2Yyrrtt

allelic pair. This is 1 : 2 . 1 if dominance is complete. The three monohybrid ratios are then combined as illustrated in figure 3.12. The results are summarised in figure 3.13 in which both the genotypic and phenotypic ratios of the F_2 generation are given. *It* will be observed that the F_2 generation consists of 27 genotype classes which fall under 8 phenotype classes in the ratio of 27 · 9 : 9 : 9 : 3 : 3 : 3 : 1.

As the number of characters for which an organism is hybrid goes on increasing the hybrid becomes more complex, its gametes and the phenotypes in the F_2 generation more diversified. These can be worked out for the polyhybrids by the "forked-line" method which is essentially the same as that used for the trihybrids. The relation between the number of allelic pairs involved in a cross, the number of different kinds of gametes formed by the F_1 hybrid and the number of phenotype and genotype classes in the F_2 generation are given below :

TABLE 3.2. Relation between the number of alleles involved in a cross and the number of phenotypic and genotypic classes in F_2.

No. of allelic pairs involved in the cross	No. of different kinds of gametes formed by the F_1 hybrid	No. of phenotypic classes in the F_2 generation if dominance is complete	No. of genotypic classes in the F_2 generation	No. of possible combination of F_1 gametes	
n	2^n	2^n	3^n	4^n	
1	2	2	3	4	Tested by Mendel for Peas and found correct
2	4	4	9	16	
3	8	8	27	64	
4	16	16	81	256	calculated
5	32	32	243	1024	
6	64	64	729	4096	
10	1024	1024	59049	1048576	"

PRACTICAL APPLICATION OF INDEPENDENT SEGREGATION

A reference to the dihybrid ratio will show that the progeny of the F_1 dihybrid consists of four phenotypes. Two of these have

the same combination of characters as the parents but two are of new types. The new types are produced as a result of recombination of the characters of the parents. The F_2 of a trihybrid cross shows six new combinations. Knowledge of the basic Mendelian principles tells us in advance the new combinations that will appear in the progeny of hybrids and enables us to predict their frequency. This is of great importance to the plant breeder. New types of plants having new combinations of useful characters can be produced by hybridisation and further breeding. In fact, the plant breeder can set before himself a goal and proceed to produce plants to order by recombinations.

SUMMARY OF MENDEL'S IDEAS

Mendel's work and his ideas on heredity may be summarised as follows :

(1) Traits appear in two alternative forms such as tall stem and dwarf stem, coloured flowers or white flowers, round seeds or wrinkled seeds, etc. Such contrasting pairs of characters are now called *allelomorphs* or *alleles*.

(2) Every trait in an organism is determined by a single pair of hereditary units, which are now called genes.

(3) One member of each contrasting pair, the *dominant*, could completely mask the other or *recessive* trait in a cross.

(4) When an organism which contains both members of an allelic pair forms gametes, the two members of a pair do not fuse or mix but separate or *segregate* from each other, so that each gamete carries only one of them. In other words, a gamete is *pure* for a character.

(5) Every character is inherited independently of every other character. In other words, the different maternal and parental characters (or their genes) do not stay together in the offspring of the hybrid but enter into new combination in the gametes. The result is that in each generation a random *recombination* of characters or their genes takes place. This recombination is a matter of pure chance, so that when there are many offspring every possible combination of characters is produced.

The principles of *segregation* and *recombination* were Mendel's original contribution to the phenomena of heredity and have been confirmed repeatedly in a great variety of plants and animals. The principles of segregation and independent recombination are basic

foundations of Mendelian heredity. The principle of independent recombination, although basically true, has its limitations.

WHY MENDEL SUCCEEDED

Having considered at some length Mendel's methods and his results, it is time to say a word as to the causes of his success in a field in which many people before him had ventured but failed. In evaluating the work of Mendel it should be remembered that he was not a biologist but a monk who had some training in mathematics and physics.

Mendel's predecessors in hybridisation experiments had considered the organism as a whole and studied the inheritance of all the characters at once. This caused confusion and made matters complicated. Mendel simplified the problem and studied the inheritance of isolated single characters at a time. Having done that, he studied the behaviour of two characters together at a time. In all his experiments, Mendel carefully counted the numbers of each type of offspring and kept statistical records of successive generations with the accuracy of a mathematician. He thus knew the pedigree of his plants. As a result of this technique, the phenomena of inheritance were reduced to a mathematical problem. His clear and critical mind was a great asset in solving this problem. In this, perhaps, his training in mathematics was also helpful. More important than these factors was that dame luck was smiling upon Mendel. It was a fortuitous stroke of good luck that he selected garden pea as a material for his experiments. Of this plant there were several distinct cultivated varieties which differed from one another in a few characters only. The selection of the characters with which he worked was equally fortunate as they showed complete dominance. The flowers of pea are normally self-pollinated. Self-pollination could be prevented by opening the covering petals of the flowers and removing the stamens before the anthers had ripened and burst. The stigma of this emasculated flower could then be pollinated by pollen from another plant which was desired to be used as the male parent in a cross. Mendel adopted this very procedure in his experiments on hybridisation He also took care to cover the flowers thus pollinated to prevent contamination by pollen of unknown origin by insects. To obtain the F_2 generation all he had to do was to allow the flowers to self-pollinate.

QUESTIONS

Note. In garden peas, yellow seed colour (Y) is dominant over green (y) and round seed shape (R) dominant over wrinkled (r). The two character pairs segregate independently.

1. A pure yellow wrinkled variety is crossed to pure green round. Give the phenotypes and genotypes of F_1, of the gametes of P and F_1, and the F_2 phenotypic ratio. Will it make any difference to the F_2 ratio if the parents involved in the cross are pure yellow round and green wrinkled ?
2. What gametes will be formed by the pea plants involved in the following crosses ? Determine the phenotype ratio of the offspring from each cross

$YyRr \times yyrr$	$YyRR \times yyrr$
$YyRr \times YyRR$	$YvRr \times Yyrr$
$YYrr - yyRR$	$YvRr \times YyRr$

3. A yellow round × yellow wrinkled cross gives a green wrinkled offspring. Give the genotype of the parents. What other offspring may be expected from this cross and in what proportion ?
4. In guinea pigs, rough coat (R) is dominant over smooth coat (r), and black coat (B) is dominant over white (b). A homozygous smooth black animal is crossed with homozygous rough white. Give the appearance of F_1 and F_2.
5. The F_1 of the previous question is crossed with a homozygous rough black animal ; with a smooth white one Give the phenotypes of the offspring in each case.

4

AFTER MENDEL

INCOMPLETE DOMINANCE

THE early years of the twentieth century were a period of testing After the rediscovery of Mendel's work in 1900, thousands of experiments were conducted by biologists on the most diverse groups of plants and animals to test Mendel's conclusions. The result was a general confirmation of Mendel's laws. But it was soon discovered that all the cases investigated did not conform to the law of dominance and independent assortment and some modification of them became necessary. The law of segregation of characters has, however, stood the test of time and remains unchanged to this day.

Mendel had studied in all seven pairs of alternative characters in the garden pea and in all the cases he found that when he crossed plants showing opposite characters of a pair, all the F_1 plants showed only one character of a pair. For example, in a tall× dwarf cross, all offspring were tall. In other words, dominance was complete. Complete dominance is, however, not universal. There are many cases which show **no dominance** or only show **incomplete dominance** so that the hybrid individuals are more or less intermediate between the parents. For example, when a red-flowered variety of four o'clock plant, *Mirabilis jalapa*, is crossed with a white-flowered variety, all the F_1 plants are pink-flowered. The F_2 generation consists of reds, pinks, and whites in the ratio of 1 : 2 : 1 as shown in figure 4.1. The reds and whites breed true but the pinks again produce the three kinds. In the case of sweet pea and snapdragon (*Antirrhinum majus*) also, a cross between a

red-flowered and a white-flowered variety produces pink-flowered F_1 generation and an F_2 generation of red, pink and white-flowered plants in the ratio of 1 : 2 : 1. A similar case occurs in the blue Andalusian fowl. The offspring of a black×white cross have a mixture of black and white in their feathers, which presents a a slate-blue appearance. When blues are mated with each other, the F_2 generation consists of blacks, blues and whites in the ratio 1 : 2 : 1 While the blacks and whites breed true, the blues on

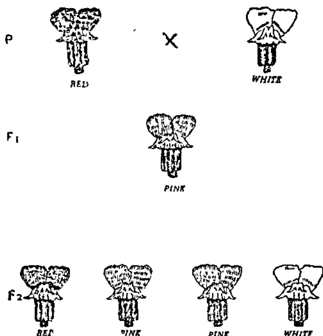
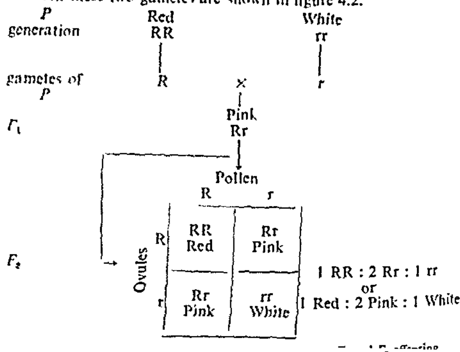


Fig 4.1. Inheritance of flower colour in the snapdragon. The hybrid from crossing red and white-flowered plants is intermediate (pink) in colour and upon selfing gives three kinds of plants in the F_2 generation

inbreeding invariably produce the three kinds like their F_1 ancestors. They a [illegible] l true. This kind of inher [illegible] ther example is met with [illegible] red and a white type are crossed the F_1 hybrid is roan in colour which is intermediate between the parental types. The roan colour is caused by a fine mixture of hairs of red and white in a mosaic fashion.

These and other similar cases are explained on the basis of Mendelian segregation. In the case of four o'clock plant, the original red and white parents carry the factors RR and rr respectively.

The F_1 hybrid will have the genotype *Rr*. This will form two kinds of male and female gametes, some carrying the factor *R* and an equal number carrying the factor *r*. The results of chance union between these two gametes are shown in figure 4.2.



phenotype. *RR* homozygous is red and the *rr* homozygous is white. The heterozygotes *Rr* are phenotypically different from both homozygotes. They are pink because the genes *R* and *r* have about equal effect, there being no dominance of the one over the other. The result is an intermediate character of the hybrid. The phenotypic ratio of the F_2 generation is the same as the genotypic ratio.

Numerous examples of incomplete dominance have been discovered in crop plants. In cotton, the cross Hairy leaves × Glabrous leaves gives F_1 hybrids which are only slightly hairy. The F_2 consists of 1 very Hairy : 2 Hairy : 1 Glabrous. In radishes the F_1 hybrids of a cross, Long root tubers × Round tubers, are intermediate and the F_2 consists of 1 Long tuber : 2 Intermediate tubers : 1 Round tuber. *In rice the character clustered spikelets* (*CC*) is incompletely dominant over non-clustered (*cc*). The F_1 hybrid (*Cc*) has intermediate clusters and the F_2 consists of 1 clustered spikelet : 2 intermediates : 1 non-clustered types

In a dihybrid cross the ratio 9 : 3 : 3 : 1 in the F_2 generation is found only when both characters show complete dominance. Where only one character shows complete dominance and the other shows incomplete dominance, the F_2 ratio is modified and gives six phenotypes in the ratio of 3 : 6 : 3 : 1 . 2 : 1. This may be illustrated from inheritance in rice. Here lax panicle (*S*) is completely dominant over dense panicle (*s*) giving a typical 3 : 1 phenotype ratio in the F_2. The character clustered spikelets (*C*) is incompletely dominant over non-clustered (*c*) giving a phenotype ratio of 1 clustered 2 intermediate : 1 non-clustered types. The F_1 hybrid of a cross involving both these characters (*SsCc*) has lax panicle with intermediate clusters of spikelets. The F_2 will give the phenotype and genotype ratios given in Table 4.1.

TABLE 4.1 Phenotypic and genotypic dihybrid ratio in rice in which one character (lax panicle) shows complete dominance and the other (clustered spikelet) shows incomplete dominance

Phenotypes	Genotypes	Genotypic frequency	Phenotypic ratio
Lax, cluster	SSCC SsCC	1 2	3
Lax, int	SSCc SsCc	2 4	6
Lax, no cluster	SScc Sscc	1 2	3
Dense, cluster	ssCC	1	1
Dense, inter	ssCc	2	2
Dense, no cluster	sscc	1	1

The students may check the above ratio by making a 16-square checkerboard or by the forked-line method.

Where both the characters in a dihybrid cross show incomplete dominance each genotype in the F_2 generation has a distinct phenotype, there being nine different genotypes and nine phenotypes. To take an example, in the snapdragon red flowers and broad leaves (*RRBB*) are both incompletely dominant over white flowers and narrow leaves (*rrbb*) the F_1 hybrid (*RrBb*) has pink flowers, intermediate leaves. The F_2 gives the phenotypic ratio of

1 : 2 : 1 : 2 : 4 : 2 : 1 : 2 : 1. This is a modification of 9 : 3 : 3 : 1 ratio. The results of this cross are illustrated in figure 4.3 and summarised in Table 4.2.

P generation — Red broad *RRBB* — White narrow *rrbb*

Gametes of *P* — *RB* × *rb*

F_1 — Intermediate pink *RrBb*

Pollen

Ovules	RB	Rb	rB	rb
RB	RRBB Red broad	RRBb Red inter	RrBB Pink broad	RrBb Pink inter
Rb	RRBb Red inter	RRbb Red narrow	RrBb Pink inter	Rrbb Pink narrow
rB	RrBB Pink broad	RrBb Pink inter	rrBB White broad	rrBb White inter
rb	RrBb Pink inter	Rrbb Pink narrow	rrBb White inter	rrbb Pink white

Fig 4.3. Result of a dihybrid cross between a snapdragon variety with red flowers and broad leaves and another with white flowers and narrow leaves, both characters showing intermediate inheritance

TABLE 4.2. Summary of figure 4.3, showing the genotypic and phenotypic ratio in a dihybrid cross in which both characters show incomplete dominance.

Phenotypes	Genotypes	Genotypic frequency	Phenotypic ratio
Red broad	RRBB	1	1
Red inter	RRBb	2	2
Red narrow	RRbb	1	1
Pink broad	RrBB	2	2
Pink inter	RrBb	4	4
Pink narrow	Rrbb	2	2
White broad	rrBB	1	1
White inter	rrBb	2	2
White narrow	rrbb	1	1

To sum up, the relation between the number of factor pairs showing incomplete dominance and the number of phenotype and genotype classes in the F_2 are shown in the table given below :

No. of factor pairs in a cross showing incomplete dominance	No of different kinds of gametes formed by F_1	No. of phenotype classes in F_2 in case of incomplete dominance	Homozygous classes	Heterozygous types
1	2	3	2	2
2	4	9	4	12
3	8	27	8	56
n	2^n	3^n	2^n	4^n-2^n

An interesting case of incomplete dominance is met with in the carnations. In plants, single flowers are, in general, dominant over double flowers. This is the case, for example, in primulas, poppies and larkspurs. But in some cases, in carnations for example, the heterozygote is intermediate. A good commercial double type is generally heterozygous producing when selfed three types, namely singles, extremely double types ("busters"), and intermediates. The

first two are homozygous and breed true, and the last is heterozygous like the parent.

In still other cases, dominance may be wholly incomplete so that the hybrid offspring may show a greater (but not exact) resemblance to one parent than to the other. There may thus be intermediate conditions between complete dominance and no dominance at all; and these various conditions may be found among the different traits of a single individual. In all cases, however, where the parents belong to true breeding varieties, the F_1 hybrids are all uniform in their hereditary traits.

From the above account of incomplete dominance it would be clear that dominance should be regarded *not as a law but as a* phenomenon. In fact the cases of incomplete dominance are far more numerous than those of complete dominance. There may be an impression in the minds of some that the Mendelian principle is the "law" of dominance. The cases of incomplete dominance cited above should remove this erroneous idea as also the wrong idea that the 3 : 1 ratio is the Mendelian principle. The real *Mendelian principle is the segregation of alleles without admixture in the hybrid*

THE MYSTERY OF DOMINANCE

The conception of dominance explains, for example, why the offspring of a tall×dwarf cross are all tall. This, however, does not explain why tall should be dominant over dwarf; why is dwarf not dominant over tall or white flower colour over red. Our present knowledge about the action of genes is so imperfect that a really good explanation of dominance is not possible. All that we can say is that, for instance in the pea plant, one gene for tallness

t of the plant.

vhen we note that

in one species, it

cond species. For

llow in peas ; but

yellow fruit colour is dominant over green in the squash. Similarly, black is dominant over white in rabbits and guinea pigs. But, on the contrary, white is dominant over black in the leghorn chicken. Cases of incomplete dominance as in the Andalusian fowl and the four o'clock plant make matters still more confusing.

trait in an organism completely overshadows its

allele, it does not mean that every trait in that organism will show complete dominance. For example, in man brown eye colour completely dominates over blue eye colour, but skin colour shows incomplete dominance.

It is evident that the causes of dominance are shrouded in mystery. Yet, in some cases, it has been possible to give a satisfactory explanation as to why one trait dominates over its opposite. These cases, few as they are, are instructive.

1. Why Black is Dominant over White in Rabbits. In rabbits, a pure black × white cross always gives black offspring, showing that black is the dominant trait. The black colour is due to the presence of the pigment melanin in the hair. This pigment is absent in the white rabbits. Melanin can be produced from the *amino-acid tyrosine by the action of the enzyme tyrosinase.* The amino-acid is obtained from the food by both types of rabbits. Yet only black rabbits produce melanin. This is because only black rabbits can produce tyrosinase. The production of the enzyme is controlled by a gene which is present in the black rabbit and absent in the white rabbit. One gene for the production of tyrosinase is enough to convert tyrosine to melanin. That explains why the heterozygote is black. The homozygous white lacks this gene altogether and cannot produce melanin from tyrosine and consequently fails to develop the black colour.

2. Why Normal Body Size is Dominant over Dwarf in Mice. There is a variety of true breeding dwarf mice and a variety of true breeding normal size mice. When the two varieties are mated, all the F_1 offspring are of normal size. This means that normal size is dominant over dwarf size. It was found that the normal size mice had a larger pituitary gland than the other type. Now, the

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for

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through their action on the pituitary gland. The following experiment confirms this hypothesis. Pituitary tissue from normal size mice was engrafted into some baby dwarf mice and they grew to

norma

mone

fore,

The dwarf mice (*nn*) lack the *N* gene and are consequently deficient in growth.

3. **Alkaptonuria.** In some people, the urine turns black on exposure to air. This defect is inherited as a recessive to normal. The urine of people suffering from alkaptonuria contains a substance called alkapton which is entirely absent from the urine of normal people. It is this substance that causes the urine to blacken. It was discovered that the blood of normal people contained an enzyme which oxidised alkapton (homogenetisic acid) so that it is excreted as carbon dioxide and water, hence their normal urine. This enzyme was not present in the blood of persons suffering from this defect. Hence their kidneys excreted alkapton in the urine Evidently, the gene for normal causes the enzyme to be produced One gene for normal is as good as two. Whether a person is homozygous or heterozygous for this gene, enough enzyme is produced that destroys alkapton and the urine remains normal. When the gene is altogether absent, no enzyme is produced with the result that alkapton is not destroyed and the urine turns black. The normal condition is, therefore, dominant.

LINKAGE

Mendelian ratios depend upon the independent assortment of characters. Post-Mendelian work has revealed that the law of independent assortment does not always hold true. Even Mendel was aware of this. For example, in his pea plants he found that every plant which had red flowers also had seeds with grey seedcoats, whereas every plant that had white flowers had seeds with white seedcoats. If these plants are crossed, then according to the law of independent assortment, the F_2 generation should contain some plants with red flowers and white seedcoats, and some with white flowers and grey seedcoats. Yet, these types did not appear. In the F_2 generation plants with red flowers always had grey seedcoats and these with white flowers always had white seedcoats. Mendel noted this deviation from his law but did not attempt any explanation. It is now known that the Mendelian characters of a given organism fall into a certain number of groups, all the characters in a group being inherited together as one bloc rather than independently. Characters that are inherited together as one group are said to be **linked** and the phenomenon is known as **linkage.** A group of characters that do not show independent assortment but are inherited as a single unit (*en bloc*) comprises what is called a **linkage group.** For example, in a certain variety of pea, white flowers, green leaf axils and pale coloured testas are characters

which are inherited together, *i.e.*, are linked. All the three characters are associated together in one linkage group. Similarly, coloured flowers, purple leaf axils and grey testas are linked characters in a second variety. When these varieties are crossed, we do not get in the F_2 generation a white-flowered offspring with a purple leaf axil nor a coloured-flowered offspring with a green leaf axil. Instead, only two types of offspring with the parental combinations appear in the approximate ratio of 3 : 1. The explanation is that characters in each group are in some way linked with one another. Explanation of the causes of linkage will be discussed in chapter 6.

QUESTIONS

1. In the four o'clock plant, a plant which is heterozygous for red flowers (R) and white (r) is pink What will be the flower colour of the F_2 produced from crossing these varieties ? of the F_3 ?
2. The F_2 in the previous question is crossed to the red parent, another to a white. Determine the genotypic ratios of the offspring in each case.
3. In the "Andalusian" race of fowls the gene for black feathers (B) is incompletely dominant over its allele for white feather (b), the heterozygote being slate blue. Determine the F_2 phenotype and genotype ratio of a cross between a black and a white bird. What will be the result when F_1 bird produced in the above cross is mated to a black bird ? a white bird ?
4. Is it possible to obtain true breeding races of either pink four-o'clock plants or blue Andalusian fowls (without further mutations) ? Why or why not ?
5. In snapdragons tall (T) is dominant to dwarf (t) ane red flowers (R) incompletely dominant to white (r), the hybrid being pink. A pure tall red is crossed to a pure dwarf white, and the F_1 are self-fertilized Give the F_2 phenotype ratio

5

HOW MENDELIAN PROBLEMS ARE SOLVED

In all genetic studies it is often necessary to work out theoretically the possible results of a mating. There are many different methods for calculating the Mendelian expectations. We have already described in chapter 3 the forked-line method and Punnett's checkerboard method. Mendel himself used the algebraic method described on the next page. Whichever method is employed it is important to remember the law of chance and to take into account all the possible combinations.

The first step in either method is to determine the different kinds of gametes each parent to a mating is expected to produce. It is essential that all the possible gene combinations should be represented in the gametes in their proper proportion. Some fundamental points which the student must remember in this context are (1) that gametes produced by the homozygotes are all of *one* type ; (2) that the individual which is heterozygous for one pair of alternative character (monohybrid) produces *two* kinds of gametes in equal numbers, *viz.*, dominant and recessive ; (3) that double heterozygotes (*i.e.* individuals heterozygous for two independent characters) produce four types of gametes all equally numerous ; and (4) triple heterozygotes form eight types of gametes, all equally numerous. In general, every additional character in which the individual is heterozygous doubles the assortment of gametes which it would otherwise form, as given in the table below :

Constitution of the parent	Gametes which it will form
Homozygote, AA	All A

Homozygote,	aa	all a
,,	AABB	all AB
,,	AABBCC	all ABC
,,	AAbbCC	all AbC
Heterozygote,	Aa	A+a
,,	Bb	B+b
,,	Cc	C+c
,,	AABb	AB+Ab
Double heterozygote,	AaBb	AB+Ab+aB+ab
,, ,,	AaCc	AC+Ac+aC+ac
,, ,,	BbCc	BC+Bc+bC+bc
Triple ,,	AaBbCc	ABC+ABc+AbC+aBC +Abc+aBc+abC+abc

To repeat, *the essential point about which the student must be very clear in his mind is to know what kinds of gametes each parent will form.* This is the crux of the whole problem and involves the application of Mendel's two laws. A quick method for this is the forked-line method. Subsequent steps in the calculation are a comparatively easy matter.

ALGEBRAIC METHOD

First determine the kinds of gametes formed by either parent. The gametic combination of one parent is then multiplied with that of the other as in algebra and the product gives you the theoretical results to be expected among the offspring.

Let us first consider only one trait. A pure tall plant (*TT*) is crossed with a dwarf plant (*tt*). The pure tall plant will form only one kind of gametes, all carrying *T*; the dwarf plant similarly forms gametes, all carrying *t*. The result of mating the two is $T \times t$ or *Tt*. This will be tall because *T* dominates over *t*. This is Mendel's F_1 hybrid. What will be the results in the F_2 generation when the F_1 hybrids are self-pollinated or pollinated amongst themselves? The male and female gametes of this hybrid will each be $(T+t)$. The result of the mating will be:

$$\begin{array}{r} (T+t) \\ \times(T+t) \\ \hline TT+Tt \\ Tt+tt \\ \hline TT \times 2Tt+tt \end{array}$$

i.e., 25% pure tall (dominant)
50% hybrid tall
25% pure dwarf (recessive)
or altogether 3 talls : one dwarf.

Let us now calculate the results to be expected if the F_1 hybrid

is backcrossed with the recessive parent. The F_1 gametes are $T+t$; the gametes of the recessive parent are all t. The backcross zygotes will be

T+t or 50% hybrid tall
×t 50% pure dwarf
Tt+tt

A cross involving two character differences is worked out as in the following problem. **What is the result of self-fertilising a pea plant which is hybrid for tall size and red flowers?**

TtRr × TtRr ⟶ ?

First work out the results for each trait separately	T+t	R+r
	T+t	R+r
	TT+2Tt+tt	RR+2Rr+rr

Then multiply the products

TT+2Tt+tt
RR+2Rr+rr

1TTRR+2TTRr+1TTrr+2TtRR+4TtRr +2Ttrr+1ttRR+2ttRr+1ttrr

This method becomes rather complicated when three or more traits are involved. In such cases it is better to use the other methods which are simpler and more efficient and at the same time interesting and popular.

DEDUCING GENOTYPES

Quite often in genetical problems it becomes necessary to *determine the genotypes of parents from the results of a particular cross*. This having been done, the probable character of additional offspring can also be determined. Such problems require the application of the principles of deductive logic as illustrated in the following examples.

Example 1. In rabbits, black (*C*) is dominant to white (*c*). A black male rabbit is mated to three females X, Y and Z. X and Y are black and Z is white. The breeding results are as follows:

Male × female X produces a black rabbit.
Male × female Y produces a white rabbit.
Male × female Z produces a white rabbit.

Determine the genotypes of the four rabbits and the colour of the offspring to be expected from further matings of the male rabbit with the three females.

Because white is recessive, all the female parents and their offspring which are phenotypically white must be homozygous. The

female rabbit Z and the offspring of Y and Z, therefore, have the genotype *cc*. All those that are phenotypically black may be homozygous or heterozygous. In any case they have at least one *C* gene. The male and the female X and Y are, therefore, *C*? Now the offspring of the male rabbit and the female Z is white-coloured *cc*. This offspring received one *c* gene from the mother and must have received the other from the father. The male rabbit is, therefore, heterozygous (*Cc*). The fact that the offspring of the mother Y is white proves that this too was heterozygous (*Cc*) because it must have transmitted one recessive gene to the offspring. The female X could be homozygous or heterozygous for the fur colour. The data in its case is insufficient and it is not possible to arrive at a decision. Further breeding is necessary to determine this. The genotypes of the different rabbits are, then, as follows :

Male =*Cc*. Y=*Cc*
Female X =*C*? Z=*cc*

Results of further breeding to be expected are as under .

Male rabbit × Female Y ⟶ 3/4 Black : 1/4 White
Cc *Cc*

Male rabbit × Female Z ⟶ 1/2 Black : 1/2 White
Cc *cc*

Example 2. In chickens the gene for rose comb (*R*) is dominant to the gene for single comb (*r*). Study the following data :

Cock A rose comb	×	Hen B rose comb	produces a rose-combed chick and also a single-combed chick.
Cock A	×	Hen C single comb	produces a single-combed chick.
Cock A	×	Hen D rose comb	produces a single-combed chick.

Applying the method of deductive logic explained above determine the genotypes of the four birds and the characters of offspring to be expected from further matings of the cock with these hens. For solution see page 61.

Example 3. In tomato, red flesh of the fruit (*R*) is dominant over yellow (*r*) ; and spherical shape (*S*) is dominant over cylindrical shape (*s*). The two allelic pairs are inherited independently. A cross red spherical × red cylindrical gave 122 red spherical, 120 red cylindrical, 39 yellow spherical and 41 yellow cylindrical. Determine the genotypes of the parents.

On approximation the phenoptype ratio of the offsping works out to 3 : 3 : 1 : 1. The question may be stated as under :

Red spherical × Red cylindrical ⟶ 3 Red sph. : 3 Red cyl. : 1 Yellow sph. : 1 Yellow cyl.

Since the cylindrical fruit shape is recessive, the red cylindrical parent and offspring and the yellow cylindrical offspring must be homozygous (*ss*) for the recessive fruit shape. Among the offsping there are some which have cylindrical fruit shape. They received one recessive gene (*s*) for fruit shape from the red cylindrical parent, and must have received the other from the second parent. The second parent red spherical, therefore, must be heterozygous (*Ss*) for the spherical fruit shape. The genotypes of the two parents, so far as fruit shape is concerned, is then settled.

Both the parents have red fruit colour. As red is dominant, both of them must have at least one *R* gene. Both the parents, therefore, are *R* ? The fact that some of the offspring are yellow (*rr*) shows that both parents are heterozygous (*Rr*) for the fruit colour. The yellow offspring received one *r* gene from one parent and the other from the other parent. The genotypes of the two parents, then, are as under :

Red spherical = *RrSs*
Red cylindrical = *Rrss*

The accuracy of this solution can be checked by working out the progeny ratio of the cross from the genotypes of the two parents.

Gametes of the parent RrSs ↓

Gametes of the parent Rrss →	RS	Rs	rS	rs
Rs	1 RRSs	2 RRss	3 RrSs	4 Rrss
rs	5 RrSs	6 Rrss	7 rrSs	8 rrss

Phenotypes		*Square numbers*		*Total*
Red spherical	=	1, 3, 5	=	3
Red cylindrical	=	2, 4, 6	=	3
Yellow spherical	=	7	=	1
Yellow cylindrical	=	8	=	1

This gives the phenotype ratio of 3 : 3 : 1 : 1 as given in the

problem. The science of genetics resembles mathematics in that it consists of a few basic principles which, once grasped, enable the student to solve a wide variety of problems. These fundamental concepts are summarised as follows. Genes remain together in a hybrid but are not altered by this association. A gamete carries only one gene, either one or the other of a pair, never both. Gametes mate at random, irrespective of the genes they contain; a male gamete carrying a *B* gene has equal chances of fertilising a *B* or a *b* female gamete.

In working out genetics problems the following procedure should be followed

1. Write down the symbols for each gene
2. Determine the genotypes of parent from the phenotypes of the offspring, if necessary.
3. Derive all kinds of gametes from the genotypes.
4. Make a checkerboard putting all the possible types of male gametes, along the top and all the possible kinds of female gametes along the side.
5. Fill in the checkerboard and read off the genotypic and phenotypic ratios among the offspring.

Students are advised to solve the numerical questions given at the end of this Chapter.

Solution to example 2 in the text. The single comb character being recessive, all the hens and chicks that are phenotypically single-combed must be homozygous. The hen *C* and the offspring of *C* and *D*, therefore, have the genotype *rr*. All those that are phenotypically rose-combed have at least one *R* gene. The cock, and the hens *B* and D are, therefore, *R* ? The fact that the offspring of the cock and hen C was single-combed proves that the cock is heterozygous (*Rr*). The single-combed chick received one *r* gene from its mother and must have received the other from its father. The fact that the offsping of the cock and hen D had a single comb proves that the hen D also was heterozygous (*Rr*). The same argument proves that the hen B also was heterozygous (*Rr*). Hence

Cock A=*Rr*	Hen C=*rr*
Hen B=*Rr*	Hen D=*Rr*

QUESTIONS

1 In man brown eye (*B*) is dominant over blue (*b*) A man and his wife, both brown eyed, beget a blue-eyed child. What are the genotypes of

the parents ?

2 The offspring of the above union (man) marries a brown-eyed woman who had a blue-eyed father, brown-eyed mother, and a blue-eyed brother. The man and woman have a brown-eyed child. *Give the genotypes of (1) the parents of man and woman, (2) the man and women, (3) their child.*

3 A blue-eyed man marries a brown-eyed woman whose mother had blue eyes. What proportion of the children would be expected to have blue eyes ?

4 In the Wyandottes breed of chickens rose comb (R) is dominant over single (r). How can we determine whether a particular rose comb bird is homozygous or heterozygous ?

Note. **In garden peas, yellow seed colour (Y) is dominant over green (y) and round seed shape (R) dominant over wrinkled (r).** *The two* **character pairs segregate independently.**

5 A pure yellow wrinkled variety is crossed to pure green round. Give the phenotypes and genotypes of F_1, of the gametes of P and F_1; and the F_2 phenotypic ratio. Will it make any difference to the F_2 ratio if the parents involved in the cross are pure yellow *round and green* wrinkled ?

6 What gametes will be formed by the pea plants involved in the following crosses ? Determine the phenotype ratio of the offspring from each cross

$YyRr \times yyrr$	$YyRR \times yyrr$
$YyRr \times YyRR$	$YyRr \times Yyrr$
$YYrr \times yyRR$	$YyRr \times YrRr$

7. A yellow round×yellow wrinkled cross gives a green wrinkled offspring. Give the genotypes of the parents. *What other offspring may be expected from this cross and in what proportion ?*

8. Yellow round×green wrinkled gave 73 yellow round and 69 yellow wrinkled. Determine the genotypes of the parents.

9 Yellow wrinkled×yellow wrinkled gave 115 yellow wrinkled and 35 green wrinkled. Give the genotypes of the parents.

10 Yellow round×yellow wrinkled gives 3/8ths. yellow round; 3/8ths. yellow wrinkled; 1/8th green round; and 1/8th. green wrinkled. Determine the genotypes of the parents.

11. Yellow round×green wrinkled gives yellow round, yellow wrinkled, green round and green wrinkled in almost equal numbers Give the genotypes of the parents.

12. *Green round*×yellow wrinkled give only yellow round. What are the genotypes of the parents ?

13 Yellow round×yellow round produces 47 yellow round, 17 yellow wrinkled; 15 green round; and 5 green wrinkled. Give the genotypes of the parents.

14. In guinea pigs, rough coat (R) is dominant over smooth coat (r); and black coat (B) is dominant over white (b). A homozygous smooth black animal is crossed with homozygous rough white. Give the appearance of F_1 and F_2.

15 The F_1 of the previous question is crossed with a homozygous rough black animal ; with a smooth white one. Give the phenotypes of the offspring in each case.

16. In man brown eye colour (B) is dominant over blue (b), and right-handedness (R) over left-handedness (r). A left-handed man has a right-handed, blue-eyed son. The latter marries a left-handed, brown-eyed woman from a family in which the brown eyes had been running for several generations. Give the phenotypes of the offspring regarding these two traits that may be expected from this union.

17. A right-handed man whose parents had been blue-eyed marries a brown-eyed, right-handed woman. Their first child is blue-eyed and left-handed What other combinations of these two traits may be expected in other children of the couple ?

18. In man brown eyes (B) are dominant to blue (b) and dark hair (D) to red (d) A man has brown eyes and red hair. He marries a woman with blue eyes and dark hair. They have a child with brown eyes and red hair, and one with blue eyes and dark hair. Give the genotypes of the parents and the offspring

19 Give the results of the following crosses in pea —

(i) Tt Rr×t t Rr (iii) t t r r×t t Rr

(ii) Tt Rr×Tt r r (iv) T T r r×T t r r.

20. In the four o'clock plant, a plant which is heterozygous for red-flowers (R) and white (r) is pink What will be the flower colour of the F_2 produced from crossing these varieties ? of the F_3 ?

21. The F_2 in the previous question is crossed to the red parent, [illegible] to a white. Determine the genotypic ratios of the offspring in [illegible]

22 In the "Andalusian" race of fowls the gene for black feather [illegible] incompletely dominant over its allele for white feather (b), the [illegible] zygote being slate blue. Determine the F_2 phenotype and [illegible] ratio of a cross between a black and a white bird. What [illegible] result when F_1 bird produced in the above cross is mated [illegible] bird ? a white bird ?

23 In snapdragons tall (T) is dominant to dwarf (t) and [illegible] incompletely dominant to white (r), the hybrid being [illegible] red is crossed to a pure dwarf white, and the F_1 are [illegible] the F_2 phenotype ratio.

24. In rice, lax panicle (S) is completely dominant [illegible] and clustered spikelet (C) is incompletely [illegible] tered (c). Give the genotype of F_1 when a [illegible] clustered spikelet is crossed to a plant with [illegible] clustered spikelets Determine the genotype [illegible] F_1 generation

25 In snapdragon, red flower (R) is incomp[illegible] (r), the hybrid (Rr) being pink-flowered [illegible] pletely dominant over narrow leaves (b) [illegible] Determine the genotypes and phenot[illegible] between red broad and white narrow

6

PHYSICAL BASIS OF HEREDITY

INHERITED characters are dependent on the action of certain genetic factors which control them. The name gene was used by Johannsen for these factors as a convenient term. In using this word he did not imply any particular theory of the nature of hereditary units. Since the time of Johannsen, the term gene has become a common byword with geneticists. Genes are self-perpetuating discrete bodies or particles of living matter that are responsible for the transmission of the bulk of inheritance from parents to the offspring. They are the units of inheritance.

In the preceding chapters we have repeatedly used the word gene causing this character and that. They are responsible for the commonly observed phenomenon that likes beget likes. It is due to these genetic factors that we resemble our parents, all human beings, and not horses, cows or plants. The question naturally arises, what the genes are and where in the organism they are located. The first part of the question is rather ticklish and will be dealt with in chapter 11. We have learnt a good deal about genes from breeding experiments with genetically different varieties of plants and animals. We know them from their effects on the traits of organisms through successive generations and from the phenomena of segregation and recombination according to the basic method devised by Mendel. The conception of genes enables us to explain satisfactorily these phenomena. Not only that. A knowledge of gene behaviour enables us to predict with a fair degree of accuracy the results that might be expected from any mating experiment. A theory which not only gives a satisfactory explanation of the observed facts, but also correctly predicts the results of experiments must be

a sound one. Because genes are discrete particles of living matter, the gene theory is also known as the particulate theory of inheritance. With Mendel's technique a particular gene can be identified only if it exists in two or more contrasting (allelic) forms. The reason for this is obviously clear. If all the pea plants were red-flowered, the existence of the gene for flower colour could never be determined, because no crosses involving flower colour would be possible. Only when the gene for flower colour occurs in two allelic forms, such as the red- and white-coloured strains, it can be studied by crossing the two strains according to Mendel's technique, and following it in the progenies. Without a character contrast, a character or its gene cannot be traced in progenies. Most of the genes occur in single form and, therefore, remain unknown and will continue to remain unknown until they change or some chemical or other method is discovered for their study. Sometimes the effect of an allele is so slight or obscure that it remains unobserved. Quite often a changed gene is eliminated by natural selection and does not persist long enough to be detected.

CHROMOSOMES AS GENE BEARERS

Let us now return to the second part of the question raised above. Where are the genes located ? When Mendel discovered the laws of inheritance, he explained them by assuming that there were certain hereditary factors in the gametes which were responsible for the transmission of parental characters to the offspring. With Mendel this was a purely theoretical conception. In his days, no mechanism was known which could explain the phenomena of segregation and independent assortment. But in the thirty-five years preceding the rediscovery of Mendel's laws great advance had been made in cytology. In the twenty-five years after that, cytology began to be linked with genetics more and more, giving birth to a branch of biology called cytogenetics. The result of this union was very significant. It led to the discovery of an actual physical mechanism which exactly fits in with the requirements of Mendel's laws. It is now generally believed that the hereditary factors or genes [illegible] nuclei of the gametes and it [illegible] hereditary material is hande[illegible] through successive generations. The chromosome theory of inheritance is the foundation of modern genetics and was perfected mainly by Thomas

Hunt Morgan and his students as a result of their remarkable work on the fruit fly, *Drosophila*. The evidence in this connection is summarised below.

1. A common feature of most plants and animals, from the simplest to the most complex ones, is the process of sexual reproduction. Sexual reproduction takes place by the fusion of two sex cells or gametes, a phenomenon called syngamy. From the resultant zygote, the new organism develops either directly or indirectly. The gametes thus constitute the only structures that link the offspring to the parents. It is, therefore, evident that all hereditary material must pass through the narrow bridge of gametes.

2. The essential feature of gametic union is the fusion of their nuclei. Except in some of the lower organisms, the gametes are of two kinds. The female gamete or egg has a large amount of cytoplasm surrounding the nucleus. The cytoplasm contains stored food which is needed later on for the development of embryo. Male gametes are much smaller, and consist principally of nucleus, the cytoplasm in their case being reduced to a minimum. The male gametes of most animals and of many plants are usually motile and are called sperms, being provided with cilia that help them to reach and penetrate the egg. In most cases, the cilia and whatever cytoplasm the sperm carries are left behind so that only its nucleus penetrates the egg and fuses with the nucleus of the egg. We have already learnt that both male and female parents have an equal share in the heredity of the offspring. As explained above, the two gametes entering in the process of syngamy are often very different from each other, the egg being much larger and containing more cytoplasm than the sperm. If both these gametes are to bring in the same heredity, and to the same extent, then it is natural to presume that they must have certain things which are similar or common to both and it must be these similar things that are the carriers of heredity. Things which are not similar must be of ... heredity. Now, the only things that ... ommon and which are similar in ... herefore, quite probable that the nucleus is concerned in heredity and that much of the cytoplasm of the e... view, being probably concern... at is to develop from the zy... This conclusion is supported by the fact that reciprocal crosses between different

plant species give similar results. Since the egg and the male gamete are unequal in their cytoplasmic content it is reasonable to conclude that the cytoplasm was not responsible for the hereditary differences between species.

Experimental evidence in this regard was adduced by Boveri. He removed the nucleus from some eggs of sea urchin and fertilized both the enucleated and the normal nucleated eggs by normal sperms from another kind of sea urchin. The enucleated eggs produced larvae which resembled the male parent and the larvae which developed from the normal eggs showed characters of both the parents. As the cytoplasm in the two kinds of eggs was

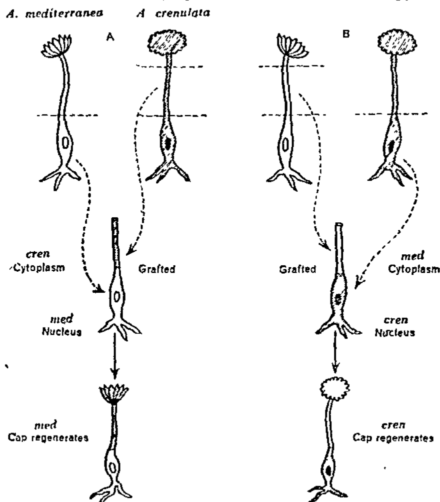


Fig. 6.1. Hammerling's grafting experiments with two species of *Acetabularia* to show nuclear control of hereditary characters

identical it can be reasonably presumed that it was the nucleus and not the cytoplasm which was responsible for the hereditary differences between the two kinds of larvae.

A conclusive evidence of the dominant role of the nucleus in heredity has been provided by the experiments of Hammerling on the marine green alga *Acetabularia*. The body consists of a rhizoidal portion from which springs up an erect stalk. The stalk has a single nucleus at the base and ends in a cap the shape of which is different in different species. In *A. mediterranea* (*med*) the cap is umbrella-shaped and in *A. crenulata* (*cren*) it is a rounded lobed structure. If the stalk above the nucleus is cut away, a new stalk and cap are often regenerated. If the stalk of the *med* type is thus removed and onto its nucleated base is grafted a *cren* stalk without nucleus, then the cap that develops is of the *med* type. If the experiment is repeated with an enucleated *med* stalk grafted to a *cren* type nucleated base then the cap that develops is of the *cren* type (Fig. 6.1). The conclusion is irresistible that it is the nucleus and not the cytoplasm that determines the hereditary character of the cap. The *med* nucleus produces a *med* cap and the *cren* nucleus produces a *cren* cap, regardless of the type of cytoplasm.

3. **Chromosomes.** The nucleus is bounded on the outside by a **nuclear membrane** which is a double layered structure made of proteins and lipids (fat). It encloses a tangled mass of fine granules and fibres called **chromatin** that lies in the nuclear sap. Besides, one or more nucleoli are also present in the nucleus. Chromatin is the most [illegible] the cell and is thought on [illegible] is of heredity. When the [illegible] age known as interphase, the chromatin appears like a network of threads with numerous granules scattered on it. But at the time of cell d[illegible] in the form of a definite number o[illegible] The number of chromos[illegible] it for a species. The small[illegible] and [illegible] chromosome consists of a spirally coiled continuous thread of [illegible] made up of nucleoprotein fibre or bundle of fibres. This is called the chromonema. The chromonema thread is marked by a number

of granular bodies arranged in a single row along its length. These are called **chromomeres**. These appear as small dense masses at irregular but fixed intervals along the length of the chromonema thread and resemble the beads on a string. When a cell is stained with basic dyes such as haematoxylin or carmine the chromatin is stained dark and the chromomeres stain darker than the chromatin threads. The chromomeres are of different sizes and shapes (Fig 6.2) and each chromosome can be differentiated from the



Fig. 6.2. Chromosomes of a plant and an animal A, *Crepis capillaris* (compositae) ; B, female *Drosophila melanogaster* (fruit fly). Each pair of chromosomes differs from every other pair in relative size and shape

other by its definite number of chromomeres and a definite sequence of large and small chromomeres following each other in a longitudinal file. Each chromosome thus has an individuality (Fig. 6.3). On account of this fixed linear arrangement of chromomeres of different sizes the chromosome is longitudinally differentiated into qualitatively different segments. Under the electron microscope, which gives a magnificati[illegible] appears as a double stru[illegible]

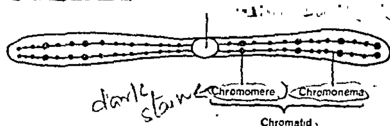


Fig. 6.3. [illegible]

twisted around each ot[illegible]
of chromomeres and is [illegible]

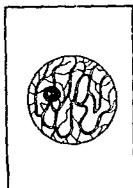
two chromatids in a chromosome. Somewhere in the chromosome is an area which does not stain dark. This clear and non-staining area is called the **centromere.** The two chromatids are attached to the centromere. The centromere plays an important role in nuclear division. Chromatin is the hereditary material. Chemically, it is composed of protein and two kinds of highly complex nucleic acids known as deoxyribonucleic acid (DNA) and ribonucleic acid (RNA).

4. **Mitosis.** A multicellular organism develops from a single-celled zygote by a remarkably uniform process of cell division which involves two distinct but co-ordinated processes The first of these is the division of the nucleus into two and is called **karyokinesis or mitosis** The second is **cytokinesis** or division of the cytoplasm into two so that each cell-half receives one nucleus, In mitosis each chromosome of the nucleus splits longitudinally into two identical halves, one going to the one and the other to the second cell. As a result of this, the two daughter cells are exactly like each other and like the parent so far, at least, as the chromosomes are concerned. The stage of the cell in which the nucleus is not undergoing division is described as **interphase.** The interphase nucleus has the typical structure described at the beginning of section 3 above. Mitosis occurs during the division of vegetative cells and may be observed in rapidly growing tissues, such as that of root tip. It is a complicated process in which the nucleus or rather the nuclear matter passes through several stages in a definite sequence. There are four principal stages in mitosis as illustrated in figure 6.4.

Prophase. This is the first stage of mitosis. In early prophase, the chromatin loses its network appearance which was characteristic of the interphase
threads begin to lose water and
untwine from one another and a
slender thread-like structures. In
threads lose more water and begin to coil spirally on themselves. As a result of this spirilisation and dehydration they become shorter and thicker. Eventually, they take the form of *short* rod-like bodies which are quite separate from one another and may be variously curved. These are the chromosomes. There number is fixed for a species. Thus, this number in the vegetative (somatic) cells of potato is 48; in onion 16; in apple 34; in garden pea 14; in maize 20; in frog 26; in rat 42;

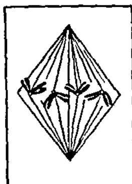
Man-46.

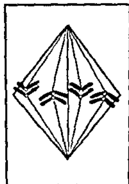
in monkey 48 ; and in man 46. The shapes and the relative sizes of the different chromosomes are also fixed for a species. Each chromosome has the structure described in the preceding section. About the end of prophase each chromosome, which has become much shorter and thicker than before, appears as a double structure consisting of two identical thread-like structures

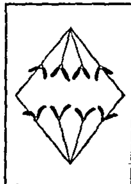

Interphase

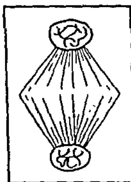

Early prophase


Late prophase


Metaphase


Early anaphase


Anaphase


Telophase


Cytokinesis Early

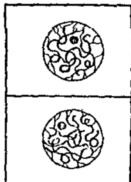

Cytokinesis

Fig. 6.4. Mitosis and cell division

called chromatids which are pressed against each other along their whole length. The two chromatids of a chromosome are independent of each other except in the region of the centromere which remains intact and to which the chromatids are attached. The parts of a chromosome between the centromere and each end are called the arms of the chromosome. Each chromatid has its own set of chromomeres so that a chromosome now has two sets of chromomeres. As the above changes are taking place the nucleoli diminish in size towards the end of this stage and disappear. The nuclear membrane also disintegrates in late prophase. Ultimately, an ellipsoidal clear area is formed around the spherical nucleus In this area, which is mainly composed of proteins, the large cellular particles like the plastids and mitochondria disappear.

Metaphase. This is the second stage of mitosis. In early metaphase ; a characteristic spindle-shaped figure appears in the nuclear region. This consists of fibrous radiations which extend from the central broad-portion called the equator and converge at two points on the opposite ends of the nuclear region, called the poles The chromosomes which were till now scattered in a random manner in the central nuclear portion of the cell begin to show peculiar movements and arrange themselves in a single plane midway between the two poles of the spindle, forming an equatorial plate. To be more precise it is [illegible] lined up at the [illegible] s a visibly dou[illegible] ngitudinally int[illegible] evelopment of the spindle and the separation of the daughter chromosomes. The chromosomes are so arranged at the equator that one chromatid of each chromosome faces one pole and the other faces the opposite pole. Two spindle fibres are attached to the centromere of each chromosome, one on either side of it. These connect the chromosome to the two opposite poles of the spindle and are called chromosomal or tactile fibres. Other fibres of the spindle extend from pole to pole and are not attached to the chromosomes. These are called the continuous spindle fibres. The spindle fibres are composed mainly of protein, some ribonucleic acid (RNA) and lipids.

The metaphase is followed by anaphase. In this stage the cen-

from [illegible]. The two [illegible] ependent of each other. The chromosomal spindle fibres now contract and the two chromatids of each chromosome are pulled apart and move towards the opposite poles. Each chromatid has now become a chromosome. According to some workers the separation of the two chromatids of a chromosome is the result of a repelling force between the centromeres of the two chromatids. At this stage, each chromosome is bent at the centromere and consists of two arms. In this poleward movement of the chromosome the centromere always leads and the rest of the chromosome follows passively (figure 6.5). As a result of this process, one set of chromosomes migrates from the equatorial plate towards one spindle pole, and an exactly duplicate set migrates to the opposite spindle pole. Each of the two sets of chromosomes so formed contains one chromatid (now a complete chromosome) from each of the double chromosomes of the original set. While the chromosomes are moving towards the poles the continuous spindle fibres lengthen and the poles move away from each other. Finally, the chromosomes appear as two groups at the two poles. The entire nuclear matter has thus been divided into two equal halves. Mitosis is, therefore, also known as **equational division** of the nucleus.

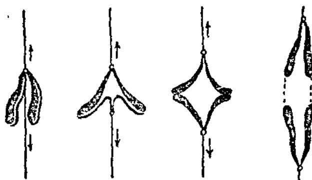


Fig. 6.5. Showing how the two chromatids of a chromosome separate during anaphase. The chromosomal fibres are shown

In the last phase, or telophase, the two groups of chromosomes assembled at the poles organise themselves into daughter nuclei, each having the same number of chromosomes as the parent nucleus. A new nuclear membrane is formed around each group. The chromosomes begin to uncoil, absorb water, elongate very much and become entangled with one another,

forming a jumbled mass which looks like a network, characteristic of the non-dividing nucleus. Nuclear sap and nucleoli are formed again in each daughter nucleus. These events are essentially the reverse of those occurring in prophase.

Nuclear division or mitosis, as it is called, is followed by the division of the cytoplasm. While the daughter nuclei are being organised at the poles, the mitotic spindle disappears except at the equator, where the continuous spindle fibres become more dense. This region is now called the **phragmoplast.** Small droplets or granular bodies, semiliquid in consistency, appear in the phragmoplast. These fuse to form in the middle of the original cell a partition called the cell plate. The droplets appear to contain pectic substances or similar cell-wall constituents. More droplets are added to the cell-plate which now begins to extend outwards until it reaches the outer walls of the original cell. This divides the cytoplasm into two roughly equal parts. Cell division is now complete and two cells are formed. The division of the cytoplasm is called **cytokinesis**. Cell division thus consists of two integrated processes. The first is the division of the nucleus and is called mitosis or karyokinesis. The second is cytokinesis or division of the cytoplasm. The two together result in the formation of two cells, each having its own nucleus.

As a result of the elaborate mechanism described above, the daughter cells come to possess the same set of chromosomes and genes as the parent. The great exactness with which each chromosome is divided quantitatively between the nuclei of the two daughter cells points to the conclusion that chromosomes are the bearers of hereditary factors. This division in fact ensures a mathematically accurate distribution of genes between the daughter cells so that the daughter cells are genetically identical to each other and to the parent cell which produced them. No structures other than those concerned in heredity would require such an exact division and distribution. In a multicellular organism, all the cells are formed from a single-celled zygote by a repetition of the process of mitosis. All these cells have identical chromosomes and genes and consequently the same heredity. When a new organism arises vegetatively or asexually, as so often happens in plants, the development of the new organism is the result of the continuation of the same process of mitosis. The result is that the organism so produced possesses the same hereditary characters as the parent,

because it has the same set of chromosomes and the same genes as the parent.

Interphase. After each division of the cell there is a period during which no mitotic activity takes place. This period between two successive divisions of a cell is called **interphase**. This may be short or long. As already stated, the late prophase and metaphase chromosome is a double structure. It appears as if it is split longitudinally into two exactly identical halves called chromatids. What has actually happened is not the division of the original chromosomes into two but that each chromosome has duplicated itself. It synthesises an exact copy of itself, which it deposits alongside. The new chromosome is identical with the original, point for point, and chromomere for chromomere. As a result of this process a mathematically precise doubling of the chromosome takes place. The synthesis of new chromosomes and genes takes place during the interphase as a preparatory step towards division. It is during interphase that nucleic acids and proteins needed for the formation of new chromosomes are synthesised. This is inferred from the fact that the amount of deoxyribose nucleic acid (DNA) present in the chromosomes is doubled during this stage. The double nature of the chromosomes is, however, not visible in the interphase stage, because the chromosomes are thin and very much elongated. It becomes visible about the end of prophase and in metaphase when the chromosomes become short and thick. Sometimes, the double nature of the chromosome is not visible even in the last stage of prophase. The interphase nucleus is often referred to as "the resting nucleus". This term is misleading as it would mean that the nucleus is in an inactive state. On the contrary, the nucleus during this period is the seat of intense metabolic activity and is, therefore, more correctly called the metabolic nucleus.

5. Meiosis. The essential feature of sexual reproduction is the fusion of two nuclei. Each gamete brings from the parent one complete set of chromosomes, called the **haploid** or **monoploid** number of chromosomes and it is written as *1N*. The resulting zygote and all of the cells of the offspring that develop from it by mitosis will, therefore, have two sets of chromosomes or the *diploid* number in their nuclei, and it is written as *2N*.

We have already stated above that the several chromosomes in a set differ from one another. Each chromosome possesses

individuality and the different chromo...
their size and s...
large chromom...
represented twice. For every chromosome contributed by the female parent there is a similar-looking chromosome contributed by the male parent, and the two are said to be homologous to each other and tog...
These carry g... ...nd
the diploid n... ...ls
are given below :

Name	Haploid (1N)	Diploid (2N)
Haplopapus gracilis (Compositae)	2	4
Pea	7	14
Potato	24	48
Onion	8	16
Apple	17	34
Maize	10	20
Wheat (Emmer group)	14	28
Wheat (Common group)	21	42
Fruit-fly	4	8
Frog	13	26
Earthworm	16	32
Rat	21	42
Monkey	24	48
Man	23	46

In course of time, the new organism reaches maturtiy and is ... metes in the case of animals ... the gametes are haploid, ...ence, during the maturation ...

and in animals at the time of gamete formation. This reduction in the chromosome number of gametes (or spores in the case of plants) is brought about by a series of two successive nuclear divisions called meiosis (Fig. 6.6).

... two successive ... livision of the ... ne wherever it ... m meiosis, it is remar...

The prophase of the first meiotic division is long and is divided into several substages. The first substage is leptotene in which the chromatin separates into the diploid number of chromosomes which appear as long and very slender threads and show numerous chromomeres of different sizes distributed at intervals along their length. The leptotene chromosomes appear to be longitudinally single.

The next substage is zygotene in which the homologous chromosomes show remarkable attraction for each other. They approach each other and unite lengthwise. This process of pairing is called synapsis. In this, the direct descendants of the chromosomes introduced by the male gamete unite lengthwise with corresponding (homologous) chromosomes similarly introduced by the female parent in the last generation. The pairing is very precise, each chromosome segment pairing only with the [illegible] homologous chromosome. [illegible] prophase, the union between the t[illegible] complete that no distinct line of separation can be seen between them. As a result of synapsis, the chromosomes become double and are called bivalents. The number of bivalents is equal to the haploid number of chromosomes. About the end of this stage the bivalent chromosomes start becoming shorter and thicker as a result of contraction and spirilisation of the chromonema threads. Sometimes, each chromosome is seen to be split into two chromatids.

[illegible] chromosome is now a four-strand structure known as tetrad and consists of four homologous chromatids. The two chromatids which belong to the same chromosome are called sister chromatids and these belonging to the two members of the bivalent are called non-sister chromatids. The undivided centromeres of the two paired chromosomes appear to repel each other with the result that the two chromosome strands are partly pulled away from each other, forming loops in some regions along their length. In this stage the bivalent chromosomes of a synaptic pair also coil round each other at certain points, holding them together and causing interchanges between non-sister chromatids of the paired chromosomes. In late diplotene stage, known as diakinesis, the

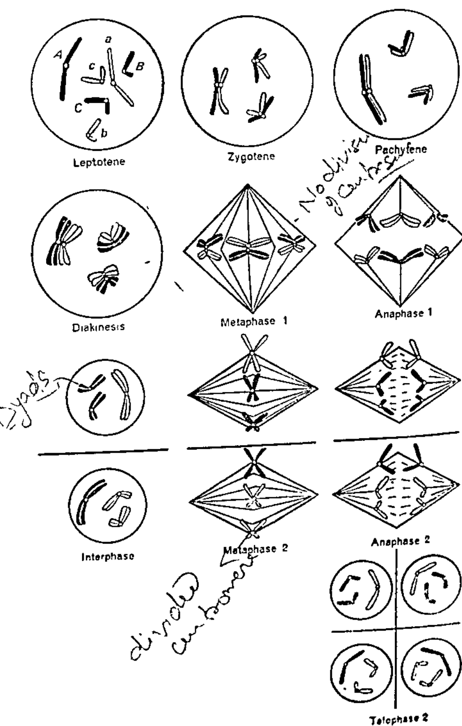


Fig. 6.6. Meiosis ; *Aa*, *Bb* and *Cc* are homologous chromosomes

tetrads become shorter and more compact as a result of further contraction. Maximum contraction of the chromosomes takes place in this stage. The chromosomes are now shorter and thicker than at the metaphase of mitosis. By the end of diakinesis, nucleoli and the nuclear membrane disappear and spindle formation takes place.

At the first metaphase the synaptic pairs of chromosomes move to the middle plane of the spindle, with the maternal chromosome in each pair facing one end, the paternal chromosome the other end of the spindle. The arrangement of the bivalents at the equatorial plate is a random one, the orientation of any one bivalent being completely independent of the orientation of every other bivalent. Each bivalent is so located that its two centromeres lie on either side of and equidistant from the equatorial plate. This appears to be a position of equilibrium. The spindle fibres are attached to the tetrads at the centromeres. In the next stage or **anaphase**, the chromosomes are pulled apart by the movement of their centromeres, which remain undivided, with the result that each tetrad breaks up into two component pairs of chromatids, or dyads. The dyads separate and move along the spindle fibres to the opposite poles. This is the true reduction division. Each daughter nucleus that is formed during **telophase** has half the number of chromosomes as compared to the parent nucleus. Unlike the mitotic anaphase each chromosome now consists of two distinctly separated chromatids united only at their centromeres. This is followed by the formation of a cell plate between the separated sets of chromosomes, dividing the mother cell into two daughter cells. Sometimes, cytokinesis fails to occur after the first meiotic division. In such cases the second meiotic division takes place in the common cytoplasm of the mother cell.

The first meiotic division is followed by an interval or **interphase**. This may be short or long or even absent altogether. After the interphase, in which the chromonema threads uncoil and elongate, a second meiotic division takes place (Figs 6.6) in which the two chromatids of each dyad separate from each other and [illegible] on of the chro- [illegible] into two each. [illegible] Because two [illegible] formation of four daughter nuclei, each containing a chromatid from every tetrad, or the reduced (haploid) number of chromosomes.

It must be noted that the chromosomes remain unchanged in longitudinal structure from the diplotene stage to the end of the second meiotic division. The duplication of each chromosome, that is, the formation of chromatids, occurs during late pachytene, but this is followed by two divisions, the first separating the homologues from each other to reduce the number of chromosomes, an event made possible because synapsis brought them together, and the second separating the two chromatids of each chromosome. When the haploid cells again unite in syngamy, the diploid number is restored.

The mechanism of meiosis, is, however, more complicated than described above (*see* page 92-93). Here it has been described in a simplified form to facilitate understanding, and for our purpose

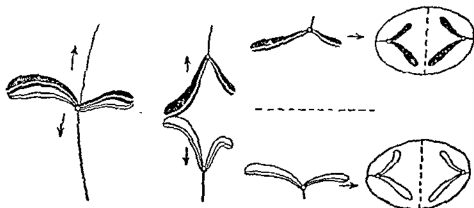


Fig. 6.7. Behaviour of a single chromosome pair during meiosis. The maternal (black) and paternal (white) chromosomes are distinguished

may be allowed to stand for the present. This mechanism is as exact as that of mitosis, only its result is different, that is, the separation of maternal and paternal chromosomes of each pair. It undoes what syngamy had achieved. It occurs in all sexually reproducing organisms, from the simplest one-celled plants and animals to the most highly organised ones. The essential features of the process are the same in all the groups of plants and animals, showing that it is a fundamental life process. In higher animals meiosis occurs dur[illegible] ...genesis. In the flowering plants it t[illegible] place when [illegible] grains and ovules are formed. T[illegible] t undergo [illegible] division are the pollen mother ce[illegible] megaspo[illegible] mother cell. In sexually re[illegible] ...ms [illegible] and meiosis occur in a defi[illegible] t to[illegible] res[illegible]

... icy in the number of chromo- ... generations. If chromosomes ... meiosis must follow syngamy as a necessary corollary In fact, Weismann had predicted its occurrence before it was actually discovered.

An important consequence of meiosis must be specially borne in mind. The arrangement of the tetrads at the spindle equator is entirely haphazard as regards their orientation. It is entirely a matter of chance whether the paternal member of a bivalent faces a particular pole or the maternal one. The position taken up by one chromosome pair does not influence in any way the position of the other pairs. Thus, if *A* and *B* are two paternal chromosomes and

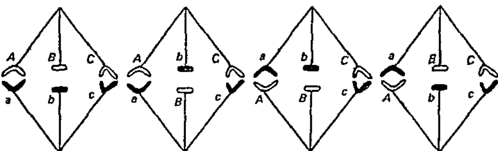
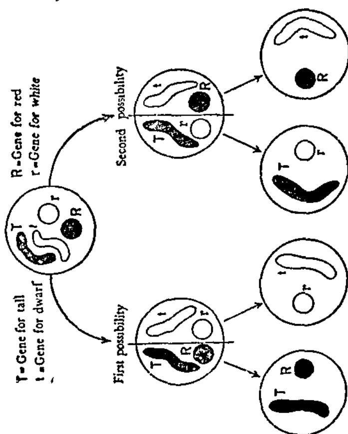


Fig 6.8 The possible arrangements of chromosomes at the end of meiosis in a cell with three pairs of chromosomes

a and *b* maternal chromosomes, at anaphase A and *a* will necessarily move to opposite poles in the first meiotic division, so also will *B* and *b* pass to opposite poles. But *A*+*B* or *A*+*b* may go to one pole. The bivalents may, therefore, separate in any possible manner. Thus, in the case of meiosis involving two pairs of chromosomes *Aa* and *Bb* the entire pool of haploid nuclei at the completion of the second meiotic division will have the chromosal combinations *A*+*B*, *A*+*b*, *a*+*B*, and *a*+*b* in equal proportion. With three chromosome pairs (*Aa*, *Bb* and *Cc*) eight different combinations are possible as shown in figure 6.8. Figure 6.6 shows one of such eight possible arrangements. It will be obvious that any resulting cell will contain only one of each maternal-paternal pair of chromosomes. In other words, in a haploid cell resulting from meiosis, it is entirely a matter of chance which, and how many, chromosomes will be maternal, and which and how many paternal. We can state this in another way. When the cells of an individual undergo meiosis, there are two ways in which a bivalent can arrange itself at the equator in the first metaphase. Both these arrangements occur with equal frequencies. Because

each bivalent does so independently of every other bivalent, the result is that the segregation which follows occurs independently for different pairs of homologous chromosomes. Considering the example given above in which two pairs of homologous chromosomes *Aa* and *Bb* are involved we find that 50% of the resulting haploid cells have the same combination of non-homologous chro-



A cell from a dihybrid parent. (Black chromosomes from male parent white from female).

At meiosis, the chromosomes of this cell may line up in either of the two ways.

When several cells are undergoing reduction division at the same time, both possibilities occur in equal numbers.

Four different types of gametes produced in equal numbers

Fig. 6.9. Chromosome behaviour during meiosis to show why a dihybrid produces four different types of gametes in equal numbers

mosomes (*AB* and *ab*) as entered the individual in the parental gametes, whereas 50% of the haploid cells carry new, non-parental combinations or recombinations (*Ab* and *aB*). Meiosis, thus brings about a recombination of chromosomes and of the genes borne on them. Such recombinations result in the fullest possible expression of the genetic potential of an interbreeding population. This cannot be achieved through mitosis. This will be further explained in the succeeding pages.

6. Chromosomes and the law of segregation The crucial points in Mendel's laws are the phenomena of segregation and independent assortment. Mendel supposed that characters were determined by certain factors of inheritance. The results of breeding experiments were explained on the assumption of segregation of these factors or genes at the time of gamete formation. No other explanation has ever been given. The ability of Mendel's assumption to correctly explain the results observed in experiments was a proof of their soundness Now, genes have never been seen. Their presence and behaviour were only inferred. Chromosomes can, however, be seen as definite and concrete bodies in the nuclei of all cells, especially at the time of cell division. Their behaviour during gamete formation and sexual union is closely parallel to the assumed behaviour of the hypothetical genes. The behaviour of the genes is, therefore, to be interpreted in terms of chromosome behaviour. Moreover, the chromosomes follow the same laws as were supposed to apply to the genes, as will be clear from the following points.

(*a*) Gene [illegible] inheritance which are no[illegible] this is also true of chrom[illegible]ation under the microscope. Each chromosome can be seen as an independent structure and each pair of chromosomes is different from every other pair. The individuality of each chromosome is not lost in the period between divisions.

(*b*) It is supposed that an organism has two genes for each trait in every body-cell. One of these came from one parent and the other from the other parent. This is equally true of the chromosomes All the chromosomes in every cell of an organism are in pairs. Of each pair of chromosomes, one is derived from one parent and the other from the other parent.

(*c*) The essential point in Mendel's presumptions is the principle of segregation. It was supposed that the two genes for a

trait which are together in an individual separate from each other at the time of gamete formation (spore formation in plants), only one member of a pair entering a gamete. This is what actually happens to the chromosomes of each pair at the time of meiosis which precedes gamete formation in animals and spore formation in plants. The two members of a pair of homologous chromosomes enter different daughter cells (gametes). The gametes, therefore, contain only one member of each pair and are pure for a chromosome as they are pure for a character (factor). This pairing and separation of two homologous chromosomes carrying corresponding characters during meiosis accounts for the segregation of characters and the phenomenon of purity of gametes. The law of segregation and purity of gametes thus finds a close parallel in the behaviour of chromosomes in meiosis and their distribution in the reproductive cells. To explain Mendel's monohybrid ratio we have only to substitute chromosomes for Mendel's factors. Thus, the law of segregation or purity of gametes and the monohybrid ratio which Mendel discovered experimentally can be explained on the basis of the facts concerning the manoeuvres of chromosomes in cell division and reproduction.

7. **Chromosomes and the** ***principle of independent assortment.*** The chromosome mechanism of inheritance also provides a physical basis for the explanation of the principle of independent assortment of characters. Let us see what happens when gametes are formed in a pea plant which is hybrid for two traits—height and flower colour. A cell from such a plant is shown in figure 6 9. The black chromosomes carry genes for *tallness* (*T*) *and red flower* colour (*R*), both dominant; the white chromosomes carry their recessive alleles for dwarfness (*t*) and white flower (*r*). During *reduction division*, homologous chromosomes synapse in pairs and line up at the equator and then the members of each synaptic pair separate from each other and each daughter cell (spore and later gamete) receives one member of each pair. Now, there are two ways in which these particular chromosomes might line up at the equator.

(*a*) Black chromosome *T* might lie on the same side of the cell as black chromosome *R*. As a result, two black chromosomes would go together into one gamete, and the two white chromosomes *t* and *r* would go together into the second gamete. The two resulting gametes will have the gene combinations *TR* and *tr*.

(*b*) Black chromosome *T* might lie on the same side as the

white chromosome *r*. Hence they would go together into one gamete, while white chromosome *t* and black chromosome *R* would go together into the second gamete, giving in the two gametes the gene combinations *Tr* and *tR*.

Since reduction division is going on in many cells at once, both of these arrangements actually occur with almost equal frequency, and, as a result, the dihybrid produces four different genetic types of gametes in approximately equal numbers. Chromosomes are thus the material structures whose behaviour makes the independent assortment of characters (or their genes) possible

Greater the number of genes involved, the greater will be the genetic variation of the gametes Thus, an organism hybrid for 1 trait (*Aa*) produces 2 types of gametes, *A* and *a* ; a dihybrid (*AaBb*) produces 4 types of gametes, *AB*, *Ab*, *aB* and *ab* ; a trihybrid produces 8 types of gametes, etc. In general, the number of types of gametes produced by an organism is equal to 2^n where n is the number of traits for which the organism is hybrid. Thus, an organism hybrid for 10 traits can produce over 1,000 kinds of gametes, and an organism hybrid for 20 traits can produce over 1,000,000 types of gametes. Since organisms are usually hybrids for hundreds of different traits, it is evident that the possibilities for genetic variation are practically boundless, and that the combination of genes carried by any particular gamete is entirely dependent on chance.

Traits are inherited independently of one another because there [illegible] produced in equal number. This random segregation of chromosomes at the first meiotic anaphase leads to random distribution of chromosomes. The resulting haploid cells would, therefore, contain a mixture of paternal and maternal chromosomes. The number of possible combinations is equal to 2^n, where n represents the haploid number of chromosomes. In man, who has 23 pairs of chromosomes the number of possible gametic chromosome combinations is 2^{23} or 8,388,608. The chances of any single sperm or egg containing only paternal or maternal chromosomes is, therefore, negligible. This recombination of genes is further increased by chiasma formation (*see* later). It should be clearly understood

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that the chromosomes contributed by a parent to one of its offspring need not necessarily remain together when this offspring forms gametes. Thus, a child that inherits genes for left-handedness and blue eyes from one parent and genes for right-handedness and brown eyes from the other parent, can pass on to the offspring any one of four combinations · (1) left-handedness and blue eyes, (2) left-handedness and brown eyes, (3) right-handedness and blue eyes, or (4) right-handedness and brown eyes. This is independent assortment of characters, and it explains why no two children inherit the same combination of traits from their parents.

The independent assortment of traits is nicely illustrated by a famous story about a couple. The wife was a beautiful dancer and the husband was an intellectual giant but far from beautiful.

"Wouldn't it be a wonderful thing for the world", said she, "if we had a child with my beauty and your brains ?"

"Yes, it would be wonderful indeed," replied her husband. "But can you imagine what a tragedy it would be if the child had my beauty and your brains !"

This is independent assortment. Even a genius cannot control the combination of traits which his children inherit. It is entirely dependent on chance.

8. **Chromosomes and genes.** The parallelism between the behaviour of genes and chromosomes is so striking that one feels amply justified in inferring that the genetic factors reside in the chromosomes. Not only is the number of chromosomes in a species constant, but the forms and identities of chromosomes are also for the most part constant. This constancy is correlated with the constancy of inherited traits in the members of a species. Alterations in the chromosome structure, removal of chromosomes or parts of chromosomes from cells or increase in their number often bring about marked changes in the hereditary characters of offspring. This is an important evidence in favour of the chromosome mechanism of heredity.

Knowledge of the structure of the chromosome obtained from cytological studies also lends support to this view. As already described on pages 68-69, a chromosome is marked by a large number of granular irregularities which are arranged in a single row on the chromonema thread much like a chain of beads on a string. These granular bodies are called chromomeres. There are several hundred chromomeres on each chromosome and their total number in a nucleus is probably always in thousands. Some chromomeres are

and these ... other. Meiosis proceeds normally ... re formed.

... has been learnt about genes and their behaviour by the discovery of giant chromosomes in the salivary glands of the fruit fly, *Drosophila* and related flies. These chromosomes are enormously enlarged and in life probably more than a 100 times as long as the ordinary mitotic chromosomes and correspondingly thick. Each of these chromosomes is a transversely striated structure, consisting of a sequence of dark staining bands separated by non-staining internodes Some bands are thicker and stain more darkly than others, while still others are mere dots (Fig 6.10). The order of bands is always the same for a particular chromosome Evidently, the bands correspond to the chromomeres of ordinary mitotic and meiotic chromosome. The gaint size of the salivary gland chromosomes is due to the fact that the gland cells grow by enlargement rather than by cell division. After mitosis the daughter chromosomes remain in the parent cell, because mitosis is not followed by cytokinesis. These daughter chromosome threads formed by repeated duplications, do not separate but remain connected and are present in a single giant chromosome. The chromosomes are thus many stranded, cable-like structures or polytenes. The bands and chromomeres both consist chiefly of nucleoprotein containing deoxyribose nucleic acid (DNA), but the interband regions consist mostly of proteins with comparatively little DNA. The distance between the bands varies. The appearance of the individual bands is often highly characteristic and distinctive. Some stain deeply, others faintly, the density of staining being not necessarily correlated with the thickness of the band, but presumably a property of its chemical structure. The number of bands on a chromosome is very large, often running into four figures.



Fig 6.10. A portion of a salivary gland chromosome of *Drosophila*, showing the banded structure

Cytological and genetical work at one time seemed to leave no serious reason to doubt that each band represents a single gene locus. This is the 'one band, one gene' hypothesis. Our modern

concept, based on electron microscopy and biochemical studies. about the relation of chromomeres and these bands to the genes will be described in chapter 11. Work on *Drosophila* shows that where certain bands on the chromosomes have been lost, there is a corresponding loss of the trait which is associated with that region of the chromosome.

According to our theory of inheritance, then, hereditary traits are due to the action of pair of genes, one member of each pair being derived from one parent and the other from the other parent. The genes are carried in paired bodies, the chromosomes, whose members are derived from the two parents; they separate from each other again when reproductive cells are formed. There are thousands of genes in an organism. They are arranged on the *chromosome in a single row like beads on a string, or possibly are* held together by chemical affinity. Each gene is a different substance, molecule or group of molecules and is capable of performing a definite part in the development of the individual such as making the flowers coloured or uncoloured, the seed-coat smooth or wrinkled, or in animals giving the eye a brown colour or blue. etc. This, in short, is the particulate theory of inheritance.

[illegible] order, not [illegible] a rule the [illegible] condition [illegible] iorten and thicken, yet the order of genes remains undisturbed, since in later generations the genes reappear in the same order and groupings.

9. **Chromosome theory and the phenomenon of linkage.** Sometimes, the genes that enter a cross together come out together as one unit. No recombination of characters takes place among the offspring of the F_1 hybrids or they appear in smaller frequencies than expected. This is a deviation from the principle of independent assortment. Evidently, random assortment of genes does not occur in such cases. This deviation from the law of independent assortment was first studied by Bateson and Punnett (1906) in sweet peas. In this plant, purple flower colour is dominant over red and long pollen grain is dominant over round. In a cross between purple long and red round the F_2 progeny did not give the 9 : 3 : 3 : 1 ratio as expected. On the other hand, purple long and red round were more numerous than expected whereas the purple round and red long were less frequent. Similarly, when a purple round variety was crossed

with a red long variety, the parental combinations appeared more frequently in the F_2 than the new combinations. At that time the relation of genes and chromosomes had not been discovered.

To explain the results of their experiments Bateson and Punnett used two terms, coupling and repulsion. The term coupling was used to denote the condition in which two dominant genes entered a cross together from the same parent and tended to remain together in the progeny. Repulsion describes a cross in which each parent contributed one dominant gene and one recessive gene and in which this combination tended to remain together in the progony. In the above crosses, the purple-long X red-round cross is an example of coupling and purple-round X red-long is an example of repulsion. These terms became obsolete when Morgan elaborated his theory that genes are borne in the chromosomes. This led to the discovery of the *phenomenon of linkage of genes* to which a *brief reference* has already been made in chapter 4. Linkage is easily explained on the basis of the chromosome hypothesis. In fact, the phenomenon of linkage of characters is an important evidence in support of the chromosome theory of inheritance.

Genetic studies have revealed that an individual possesses a very large number of genetic factors, amounting often to several thousands. The number of chromosomes in a species is much smaller, ranging from 2 pairs to over a hundred. *Evidently*, then, each chromosome must carry a plural number of genes. As the chromosomes ordinarily pass into the gametes bodily, all the genes carried on a particular chromosome will be transmitted to the same gamete as a single bloc or unit. Random assortment will not take place between genes borne in the same chromosome. Such genes are said to be linked and the phenomenon is described as linkage. In fact, if the hereditary factors are borne in the chromosomes, *the phenomenon of linkage becomes* inevitable. Genes that are linked together form a linkage group. Linkage has been observed in several species of plants and animals. The genes in a species fall into a number of linkage groups. On the chromosome theory, the number of linkage groups in any species must be equal to the number of chromosome pairs. This has been confirmed experimentally. Thus, maize has 10 pairs of chromosomes and 10 linkage groups in maize are known ; similarly, four linkage groups have been discovered in *Drosophila melanogaster* which has four pairs of chromosomes ; in *D. virilis* there are six pairs of

chromosomes and six linkage-groups. In any organism the number of linkage groups is equal to the number of chromosome pairs. If the number of characters in a linkage group is large the corresponding chromosome will be longer and will have larger number of genes than the one representing a smaller linkage group. This is what is actually observed. Large chromosomes represent large linkage groups. The only case of deviation from the principle of independent assortment is thus easily explained on the basis of the chromosome theory of inheritance. Characters will segregate independently of one another only if their genes are situated in different (non-homologous) chromosome pairs.

10. **Crossing over.** Linkage, however, is not always complete. Sometimes it fails. This may be illustrated by an example from the maize plant. Here, gene *C* for coloured seed is dominant to colourless *c*, and the gene *S* for normally filled out (full) seeds is dominant over *s*, for shrunken seeds. A coloured and full × colourless and shrunken cross gives an F_1 progeny of coloured and full seeds. The genotype of these hybrids is *CS/cs*.*

Ordinarily, that is if there is no linkage, the F_1 hybrids should produce four kinds of gametes *CS*, *Cs*, *cS* and *cs* in equal numbers. This can be tested by backcrossing the hybrid plant to the double recessive (*cs/cs*, which will form gametes of only one kind, *cs*). Such a cross should yield a backcross progeny consisting of four kinds of offspring in the approximate ratio of 1 : 1 : 1 : 1 as under :

		Gametes of F_1 hybrid (*CS/cs*)			
		CS	Cs	cS	cs
Gametes of the homozygous recessive parent *cs/cs*	cs	CS cs Coloured full	Cs cs Coloured shrunken	cS cs Coloured full	cs cs Coloured shrunken

The results actually obtained are, however, very different as will be clear from the following data from an experiment by Hutchinson:

P Coloured, full × Colourless, shrunken
CS/CS ↓ *cs/cs*

F_1 Coloured, full
CS/cs

*In the case of linked genes, the combinations are written as they enter the zygote, the combination from one parent being written above a line, and that from the other below it.

F_1 Coloured, full [CS/cs × Colourless, shrunken (Backcross) cs/cs]

↓

Backcross progeny

Coloured, full	Coloured shruken	Colourless full	Colourless shrunken	Total
CS/cs	Cs/cs	cS/cs	cs/cs	
4,032	149	152	4,035	8,368

The coloured full, and colourless shrunken seeds are approximately equally numerous and together account for about 96·4 per cent of the backcross progeny. These are the parental combinations. The recombinations, coloured shrunken, and colourless full together account for only about 3·6 per cent of the progeny. Obviously the two genes, *C-S* and *c-s* have tended to remain together in the same combinations in which they had entered the cross, that is they were linked. But how to explain the appearance of recombinations, although in much smaller numbers, in spite of the linkage ? The explanation lies in the phenomenon of crossing over between homologous chromosomes during meiosis.

In the account of meiosis given earlier, it was stated (page 80) that the facts of meiosis were more complicated than described there. What actually happens is that when homologous chromosomes synapse during meiosis, they twist on each other at the equatorial plate. At the time of their final separation, an interchange of their parts takes place so that what was part of one chromosome becomes part of another. The separating chromosomes are not the same as those that approached each other (Fig. 6.11). Each comes away with part of the other. The parts exchanged are equivalent, for the point of breakage is the same in both. Each chromosome receives from its homologue what and as much as it has lost. This is called crossing over. As a result of crossover, parts of homologous maternal and paternal chromosomes interchange, giving rise to new combination of genes or blocks of genes. That is what happened in the case of maize cited above.

The explanation of crossing over given above has been very much simplified so that it may be clearly understood. In figures 6.11 and 6.12 the crossovers have been shown to occur between whole chromosomes. These figures only give the essential idea of crossing over but are by no means an accurate picture of what actually occurs. Actually, the crossover takes place about the beginning of diplotene, when the homologous chromosomes are each divided into their chromatids so that the synapsed chromosome

pair is a four-strand tetrad. A single crossover takes place not between whole chromosomes but between two non-sister chro-

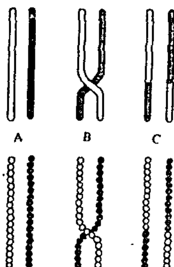


Fig. 6.11. Crossing-over in homologous chromosomes. A, before crossing-over (presynaptic), B, during crossing-over (synaptic); C, after crossing over (postsynaptic). The figures in lower row give an idea of the linear arrangement of genes

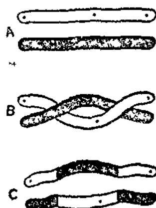


Fig. 6.12. Double crossover in a pair of homologous chromosomes; A, before B, during; C, after a double crossover

matids only (one from each homologous chromosome) as shown in figure 6.13. If the two original homologous chromosomes of a synaptic pair are designated as *ABC* and *abc* respectively, then at the four-strand stage each gene is repre-

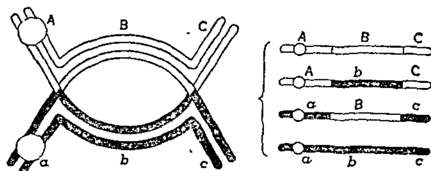
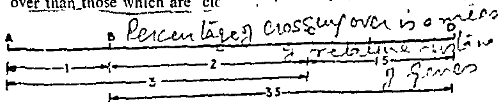


Fig. 6.13. Details of double crossover in a pair of homologous chromosomes. Left during synapsis; right, the four chromatids after the second meiotic division

sented twice If the segment *B* of one chromatid breaks, the corresponding segment *b* in a non-sister chromatid of the homologous chromosome also breaks and the broken ends rejoin. As a result of this interchange, the four chromatids will have the constitution *ABC*, *AbC*, *aBc* and *abc*. The first and the last are identical with the parental types and the middle two are new combinations. The points at which the exchange of chromatid segments takes place are known as **chiasmata** (*Sing.* chiasma). At these points the chromosomes form a cross-shaped figure. It must be remembered that in a crossover the chromatids break before they cross, not after. In other words, the formation of a chiasma (crossing of the chromosomes) is the result of crossover, not the cause of it. The number of chiasmata varies in different bivalents. Depending upon the length of the chromosomes, this number may be one, two, or three corresponding to single, double or triple crossover. In some cases no chiasmata may be formed at all. Chiasma formation breaks up linkage groups and therefore alters the set of genes which the chromosomes possessed before entering meiosis. The chromatids eventually are distributed to the four haploid cells, and it is clear that each cell (and therefore the gamete) is genetically different from every other (*see* figure 6.13).

11. **Chromosome maps.** Crossing over may occur at any point along the length of a pair of chromosomes, that is, between any two genes. The frequency of [illegible] any two genes depends upon the distance be[illegible] apart on the choromosome sh[illegible] over than those which are clo[illegible]



apart, the greater is the percentage. The percent of *crossing over is thus a measure of the relative distance of the genes from each other.* To take an example, if in the case of genes A, B and C there is 1 per cent of crossing over between the genes A and B and 2 per cent between B and C then we say that the distance between A and B is one "unit" and between B and C two units. *If the percentage of crossing over between A and C is 3 then these genes are three units apart.* In other words, *the percentage of crossing*

and another in which fuzzy seed is combined with high ginning. A combination of naked seed and high ginning will be the most desirable. Attempts to obtain this combination through hybridisation do not succeed due to the complete linkage of the two character pairs in the parental varieties.

Linkage also has its advantage. Sometimes, qualitative characters such as leaf shape, stem colour etc. are linked with quantitative characters such as size of fruit, weight of seed, or large yield. When plants are crossed, the occurrence of the easily recognisable qualitative characters in the progeny can serve as an index of the linked quantitative characters for selection purpose because the entire group of linked genes will be inherited as a block except, of course, when the linkage is broken by crossing over. Such genes are called marker genes. Thus, in cotton lint colour serves as a marker for lint length ; in rice anthocyanin pigment is marker for yield, and grain colour for weight of grain. Similarly, in millet wavy blade is closely linked with big panicles, broad leaves and thick stems.

Som [illegible] acters is due to physiological a [illegible] es there is no hope of obtaini [illegible] are varieties with tall stems [illegible] ith short stems and short duration and the chances of obtaining tall varieties with short duration are remote. Similarly, in South Indian rice a combination of high yield and short duration could not be achieved.

Some more examples of linked characters in crop plants are given below :

Maize. *Sugary endosperm and white seedlings ; coloured pericarp and full endosperm ; shrunken endosperm and white seedlings ; dwarf and shrunken endosperm ; yellow endosperm and purple plant colour : yellow endosperm and yellowish leaf ; yellow seedling and golden plant ; brown aleurone and glossy seedling ; brown aleurone and pale green seedlings ; ragged and defective endosperm ; crinky leaf and defective endosperm.*

Great millet (*Sorghum*). Loose panicle and pearly grain ; compact panicle and chalky grain ; brown pericarp and pearly grain ; awnless and stigma basal feathered ; long awn and stigma fully feathered ; white seedling and red coleoptile ; purple plant colour and purple coleoptile ; purple coleoptile and brown pericarp ; yellow seedling and waxy endosperm.

have, however, only one X-chromosome and its mate is dissimilar and called the Y-chromosome. In meiosis, the X and Y synapse and form an unequal bivalent. The two later on segregate and go to different daughter nuclei. Two types of sperms are formed, some carrying the X and an equal number the Y chromosome. The male is thus again heterogametic. If an egg is fertilised by an X-carrying sperm, the result is an XX offsping, a female. Fertilisation by a Y-carrying sperm gives an XY combination and the offspring is male.

(*c*) **'XY female' mechanism.** In birds, moths and some fishes, the arrangement is quite the opposite of above. Here it is the female that is heterogametic (XY) and produces two types of eggs, half carrying the X and the other half, the Y-chromosome. The males are homogametic being XX, and produce only one kind of sperms, all carrying an X-chromosome. Fertilization of an X-carrying egg produces a male and of the Y-bearing egg, a female.

13. **Sex-linked inherita**[illegible]ides, transmitting sex also carry g[illegible]enes are said to be sex linked. T[illegible]ance to the chromosome theory. To explain the peculiar pattern of sex-linked inheritance we will select an example from human inheritance. Some people suffer from the dread disease, *haemophilia* in which the blood does not clot normally. This disease has become famous on account of its occurrence in some of the royal houses of Europe, where it has been traced back to Queen Victoria of England. Only in 1938 one of its victims was Count *Covadonga*, a son of King Alfanso of Spain and a great grandson of Queen Victoria on his mother's side. He had received minor injuries on his face in a motor accident in America, as a result of which he bled to death under the eyes of eminent surgeons. Strangely enough, the disease appears *only in men*, but they cannot transmit the condition to their sons. They can, however, transmit the disease to their grandsons through their daughters. This trait thus alternates from one sex to the other in successive generations. This type of *criss-cross* inheritance remained a mystery until it was discovered that the gene for this disease, which is inherited as a recessive to normal, resides only in the X-chromosome. The Y-chromosome carries no gene for this trait. Let the gene for normal clotting of blood be represented by X_n and its recessive allele for haemophilia by X_h. The genotypes for the different types of males and females will be as follows :

	Normal	Haemophiliac	Carrier
Male	X_nY	X_hY	×
Female	X_nX_n	X_hX_h	X_nX_h

The progeny of a marriage between a haemophiliac man and normal woman is shown in figure 6.14. All the sons are normal because they receive the normal gene X_n from the mother and a Y-chromosome from the father which contains no gene for this trait. All the daughters will have the genotype X_nX_h. A female with this genotype will not be a bleeder, because of the dominant normal gene X_n but she can pass on the trait to half of her sons, even when she marries a normal man as will be clear from figure 6.15. It will be clear that theoretically 50 per cent sons will be normal (X_nY) and 50 per cent will be bleeders (X_hY) ; 50 per cent

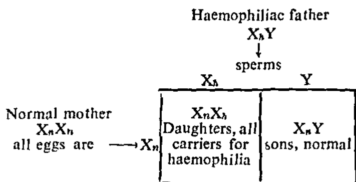


Fig. 6 14. Why a bleeder's son cannot inherit haemophilia and why his daughter becomes a carrier of haemophilia

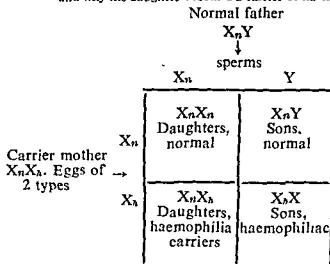


Fig. 6.15. Why half the sons of a carrier woman will be bleeders

daughters will be normal (X_nX_n) and 50 per cent carriers of haemophilia (X_nX_h). No case of haemophiliac women is known. Theoretically one could be produced if a carrier woman marries a haemophiliac man as shown in figure 6.16, but such marriages are not on record.

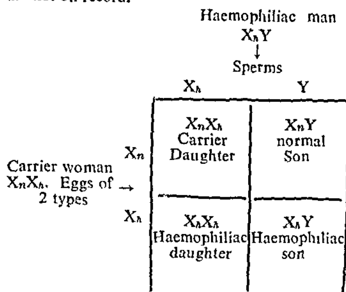


Fig 6 16. Progeny of a union between haemophiliac man and a carrier woman

A similar sex-linked character in man is colour blindness, characterised by inability to distinguish red and green colours. Both the colours appear grey. This defect is much more common in men than in women. Its inheritance follows the same criss-cross pattern. Like haemophilia, colour blindness is recessive to normal vision and passes from a man to his daughters, to his grandsons, thus skipping from male to female and then to male. Using the symbol X_+ for normal sight and X_c for its recessive allele for colour blindness we can represent the genotypes of the different types of males and females as under :

	Normal	Colour blind	Carrier
Male	X_+Y	X_cY	×
Female	X_+X_+	X_cX_c	X_+X_c

Let the readers themselves determine the results of marriages between different types of individuals. Many other examples of sex-linked characters in man are now known. These include degeneration of the optic nerves, juvenile glaucoma, myopia (short-sightedness), double eyelashes, degeneration of certain muscles and a type of valvular heart disease. This type of inheritance is known

in many organisms, both plants and animals, and is characteristic of sex-linked traits.

As already stated, genes situated in the X-chromosome have no alleles in the Y-chromosome. The Y-chromosome is comparatively inert. But there are a few genes which are peculiar to the Y-chromosome; these have no alleles in the X-chromosome. These genes are called **holandric** and the traits controlled by them appear only in males. Such inheritance is called **one-sided inheritance**. Only three or four holandric genes are known in man. One of these causes very hairy ears and another results in "porcupine skin" in which the skin over most of the body becomes thick and very rough. Some genes have alleles both in the X and in the Y chromosome. They show only partial sex-linkage.

From what has been said in this chapter, we may conclude that the Mendelian phenomena are the understandable results of the behaviour of chromosomes. What Mendel had inferred from the results of his experiments can now be explained in terms of the science of cytology. The phenomena of segregation and recombination are to be interpreted as the accompaniments of the separation and reshuffling of the genes brought about by the separation of homologous chromosomes in meiosis.

QUESTIONS

1. Describe the structure of a chromosome.
2. "Each chromosome has an individuality." Elucidate this statement.
3. Describe the meiotic division of a plant cell. What is the genetic significance of meiosis?
4. Write an essay on:

   The physical basis of heredity.

   or

   Chromosomes are the bearers of heredity.
5. What is (*a*) linkage, (*b*) crossing over? How do you explain these on the basis of the chromosome theory of inheritance?
6. How does chromosome theory of heredity explain Mendel's law of independent assortment?
7. What determines sex and how?
8. What are sex-linked characters? How are they inherited?
9. A character was reported to run through male members of a family for several generations. On what chromosome would the genes for the character be borne?
10. A character is transmitted by a man to his grandsons through his daughters and not to his sons. On what chromosome would the gene for the character be likely to be borne?
11. In man the genes for black eye (*B*) and blue eye (*b*) are borne on a pair of autosomes and colour blindness is due to a sex-linked recessive.

Two brown-eyed persons with normal vision produced a blue-eyed colour-blind son. Give the genotypes of the parents.

12. A blue-eyed woman has a brown-eyed son. The latter marries a blue-eyed woman whose father was colour blind. What proportion of sons would be blue-eyed and colour blind.
13. A normal man has a colour blind brother and a colour blind sister. Give the genotypes of the parents.
14. Man has 46 chromosomes in his body cells. If all the genes are mapped, how many linkage groups would there be ?
15. From the following distances between individual pairs of genes construct a map of the chromosome:

    r—*c*=10 units   *S*—*c*=18 units
    c—*P*=13 units   *S*—*r*=8 units
    P—*r*=3 units

16. In maize coloured endosperm (*C*) is dominant to white (*c*) and full endosperm (*S*) is dominant to shrunken (*s*). A pure coloured shrunken is crossed to a pure white full. The F_1 is then crossed to a white shrunken, and the offspring are as follows :

    Coloured shrunken=3,149
    Purple full =120
    White shrunken =115
    White full =3,334

    Give the genotypes of the *P* and F_1 and the crossover classes of gametes produced by the F_1. Calculate the distance between white and shrunken.
17. The wheat plant has 21 pairs of chromosomes. State the number of chromosomes present in the (*a*) stem tip ; (*b*) nucellus ; (*c*) pollen tube nucleus ; (*d*) embryo sac, (*e*) seed embryo, (*f*) endosperm.

7

GENE ACTION AND INTERACTION

MULTIPLE ALLELES

The various traits of an organism are determined by genes. From the view point of heredity, each individual is made up of hundreds and thousands of inheritable traits and the number of genes is also to be reckoned in thousands. Thus, a rough estimate of the number of genes in *Drosophila* puts the number between 5,000 and 15,000 pairs and in man there are perhaps 20,000 to 40,000 pairs of genes. All the genes together are responsible for determining the pattern of development at different stages in the life of an organism. The genes are distributed on the chromosomes. Each gene has a fixed location or locus on a particular chromosome. An individual receives two genes for a trait, one from each parent through the chromosomes of the sex cells. The two genes that an individual receives may be identical in their effect on the trait which they determine, when the individual is said to be homozygous, or the two genes may be unlike in their effect upon the particular trait, when the individual is said to be heterozygous or hybrid for that trait. Such unlike genes are alternative forms of the same gene and are located at the same spot in the homologous chromosomes. Genes located at the same point or locus are said to be alleles of, or allelic to, each other. Sometimes, a gene occurs in three or more forms. All these are different (mutant) forms of the same gene and are collectively called **multiple alleles**. A well-known example of multiple alleles is the gene for eye colour in *Drosophila*. Fifteen different alleles of this particular gene, located in the X-chromosome, are known. These are named, after the colour that they produce, red, eosine, apricot,

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buff, blood, cherry, honey, ivory, pearl, coral, tinged white, etc. Multiple alleles for many other characters in *Drosophila* are known, for example, shape of wings, form of wing veins, colour of body, size and shape of eyes, length of legs and characters of bristles. They have been discovered in many other insects, rats, cattle, man and other mammals and among plants in maize, evening primrose, beans and barley. It must, however, be understood that not more than two alleles can be brought into the same zygote, nor more than one into the same gamete.

The entire series of multiple alleles are represented by the same basic letter and the different forms are indicated by superscripts. Thus, in the case of eye colour of *Drosophila*, W represents the gene for red eye colour ; w^{bl}, blood ; w^{e}, eosine ; w^{a}, apricot ; w, white.

These genes form a series in which each gene is dominant to the genes following it, and recessive to those preceding it. In rabbits the coat colour is determined by a series of multiple alleles, C, c^{ch}, c^{h}, c. The gene C produces coloured coat and the homozygous recessive (cc) causes white coat. The gene c^{ch}, when homozygous, gives "Chinchella" type, a light-grey colour all over the body. The gene c^{h} in the homozygous condition produces the "Himalayan" pattern in which the rabbit's body is white, but the tips of the ears, nose, tail and legs are coloured.

MANIFOLD EFFECTS OF GENES

In all cases of Mendelian inheritance described in the preceding pages, we have always been describing a gene as causing the development of some particular trait in the organism. This seemed to imply that each pair of genes affects one and only *one trait*. This shorthand method was adopted because *it was convenient* and made explanation easy. However, this conception is incorrect. *In reality*, there is no such thing as the one-to-one relation between *a* trait and a gene. A gene often affects not a single trait, but several traits of the individual. When we speak of a gene as controlling this or that trait, we are only referring to the most obvious and easily recognisable effect of the gene ignoring the other effects which are of a minor nature but which are as much the products of the same gene as is the major effect. *From recent* investigations it would appear that most genes affect *several or* many unrelated traits of the organism that carries them. *In other* words, genes have **manifold (multiple) or pleiotropic effects.** To

cite an example from the pea plant, the same gene that affects flower colour also influences the colour of the seedcoat and the colour of the leaf axil. Similarly, the gene that determines the size of wings in *Drosophila* also affects the eye colour, character of balancers, position of dorsal bristles, the shape of spermotheca, fertility and length of life and others. The major effects of a gene may not be so important for the welfare of the individual as some of its minor effects. In the case of the *Drosophila* gene cited above, the most striking effect of the recessive allele is the production of the vestigial wings, the dominant producing the normal wings. The gene has, accordingly been named as "vestigal." To the fly, however, the effects on fertility and length of life may be more important.

Examples of pleiotropic effects of genes are quite common in the plant kingdom In lupine, the gene for flower colour also affects the height of the plant, the production of anthocyanin pigment in vegetative parts, and the character of the seedcoat. Similarly, in cotton the gene that affects the linted-lintless character also affects height, controls boll size and fertility, and determines the number of ovules per lock and viability of the seed. In sorghum the gene that controls the length of internodes also determines the length and breadth of leaves and the length of panicle.

INTERACTION OF GENES

Another idea which the reader may have got from the study of the preceding chapters on genetics is that each trait is determined by a single pair of genes. This too is incorrect. Quite often, many genes affect a single character. Thus, some 20 different genes are concerned with the pigment of the eye in the fruit fly, and more than this number are involved in the colour of the maize plant. Quite often, several pairs of genes located in different pairs of chromosomes interact to affect the production of a single trait; one pair may inhibit or reverse the effect of another pair; or a given gene may produce different effects when the environment is changed in some way. The genes are inherited as units but may interact in some complex fashion to produce the trait. This is known as **factor interaction** or **gene interaction** and often leads to modifications of the basic Mendelian ratios. A few such modifications depending upon gene interaction are described below. A modification of Mendel's monohybrid ratio due to lack of dominance was described on page 46. That should not be confused with

the cases of gene interaction here described.

1. **Lethal genes (2 : 1 ratio).** Lethal genes are those that cause such a tremendous deviation from the normal development of the individual that it is unable to survive. For example, there is a variety of mice which is yellow. The yellow coat colour is dominant to every other colour, black, brown or grey. A curious fact about the yellow mice is that they are always heterozygous for the dominant coat colour. A cross between yellow and black (or any other colour) always gives a 1 : 1 ratio of yellow and black offspring. The black offspring always breed true. When inbred, the yellow mice always give a progeny of 2 yellow : 1 black instead of the usual 3 : 1 ratio. How to explain this departure from the normal? One thing is clear from the numerical results of crosses between *yellow* and *yellow* mice. They are always heterozygous; the homozygous yellow mice do not exist and experimenters found it impossible to establish a true breeding strain for yellow coat. If we represent the dominant gene for yellow coat colour by *Y* and its recessive allele for black (or any other colour) by *y*, the heterozygous yellow will have the genotype *Yy*. A cross involving two *Yy* mice should give the following genotype and phenotype ratio among the offspring on the basis of Mendelian segregation :

1YY	:	2Yy	1yy
Pure yellow		Hybrid yellow	Pure black

Now, what happens is that the homozygous yellow offspring (YY) straightaway perish because the gene Y in the homozygous condition has a lethal effect on the embryo. These are the missing yellow coloured mice. The result is that only the last two categories of offspring are born, thus accounting for the 2 : 1 ratio. *This also explains why true breeding yellow mice do not exist.*

The "creeper" gene in fowls is lethal in the homozygous condition. This mutant gene interferes with the development of the skeleton and the embryos that are homozygous for this gene die before hatching. But the heterozygotes live to maturity. But they have deformed skeleton and are known as "creeper fowls" on account of the shortness of their legs and their gait.

Lethal genes are also found in plants. To take an example, a variety of snapdragon (*Antirrhinum*) has variegated leaves. This "golden" variety on self-pollination gives two kinds of offspring, golden and green in the ratio of 2 : 1. The green ones breed true, that is, are recessive, while the golden ones always give a mixed progeny, being invariably heterozygous. Careful germination of the

seeds of golden plants, however, reveals some feeble seedlings which are entirely yellow. These straightaway perish for want of chlorophyll. Clearly, they are the missing pure yellow zygotes.

Chlorophyll deficiencies due to lethal genes have also been reported in Indian crop plants like maize, rice and cholam. In rice a lethal recessive factor (*yy*) causes the death of the seedlings after about 8-9 days' growth, another form (*ll*), though green in the beginning, turn yellow and die off; albino (*ww*) die within a few days of germination.

In pearl millet (*Pennisetum typhoides*) green and albino seedlings were produced in the ratio of 3 : 1. The albino condition is due to a recessive factor (*cc*) and the seedlings die within a few days of germination. A case of recessive lethal green factor (*cl*) was discovered in cholam (*Sorghum caudatum*). Seedlings which were green and looked normal began to die due to atrophy of roots and shoots after one month of germination.

Many lethal genes are known in man also. These produce diseases which are fatal at different stages of development. One of these is a form of anaemia called thalassemia major which causes death early in childhood. A genetically related disease thalassemia minor is much milder and only causes some minor abnormalities in the blood. Both are due to the same mutant gene. The fatal form is due to homozygous condition of the mutant gene and the milder form due to heterozygous condition. Another one is brachyphalangy (short fingers) due to a dominant gene. A child homozygous for this condition, born to a couple both of whom have this defect (heterozygous), has no fingers or toes and dies immediately.

2. **Crosses involving two factor pairs affecting the same trait (comb types in chickens).** The dihybrid crosses described in chapter 3 dealt with two factor pairs, each pertaining to a different trait. Sometimes, two or more pairs of genes may affect the same trait in different manners. The ultimate phenotype in such cases will be due to the interaction of these genes. An example of this type is the inheritance of comb types in fowls studied by Bateson and Punnett.

In fowls, different breeds differ in their comb shape. The Wyandottes have a *rose* type comb; Brahmas have a *pea* comb and Leghorns have *single* combs. When the first two varieties are crossed all the F_1 hybrids have a new type of comb called *walnut*. Pea and rose are due to dominant genes in separate chromosomes

and single comb is recessive to them. If the dominant genes, pea and rose are represented by P and R respectively, the genotypes of the three homozygous forms will be as under :

Pea=$PPrr$, Rose=$RRpp$, Single=$pprr$







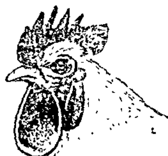


Fig 7.1. Comb shapes in chickens

When the pea and rose types are crossed the F_1 hybrid will have the genotype $PpRr$. Here both the dominants come together and each will affect the comb type in its own way and the resultant effect of combined action of P and R is a new type of comb called *walnut*. The F_1 walnut will produce four kinds of gametes : PR, Pr, pR, pr, and the F_2 progeny will produce walnuts, pea, rose and single in the ratio of 9 : 3 : 3 : 1 as shown in the figure 7.2.

The same results would be obtained by a cross between pure walnut ($PPRR$) and a single ($pprr$).

P generation	Pea PPrr		Rose ppRR
Gametes of P	Pr	X	pR
F_1		Walnut PpRr	

Pollen of F_1

Ovules of F_1	PR	Pr	pR	pr
PR	PPRR Walnut	PPRr Walnut	PpRR Walnut	PpRr Walnut
Pr	PPRr Walnut	PPrr Pea	PpRr Walnut	Pprr Pea
pR	PpRR Walnut	PpRr Walnut	ppRR Rose	ppRr Rose
pr	PpRr Walnut	Pprr Pea	ppRr Rose	pprr Single

Fig. 7.2. The cross of pea × rose comb chickens

3. **Complementary genes (9 : 7 ratio).** Sometimes, a trait is produced by the interaction of two or more dominant genes, situated in separate chromosomes which complement one another. Thus, when two certain white-flowered varieties of sweet-peas are crossed with each other, they produce F_1 plants which are red-flowered. When the F_1 plants are self-pollinated, the F_2 generation consists of red-flowered and white-flowered plants in the ratio of 9 : 7 (Fig. 7.3). This is a modification of the normal dihybrid ratio (9 : 3 : 3 : 1). Here, the formation of the red anthocyanin pigment depends upon two independent factors. Both of these must be present before the red colour is formed, neither by itself producing the colour. One of these factors (C) seems to produce

a colour base, while the second (R) produces an enzyme which activates the colour base to produce colour. One of the white-

	CR	Cr	cR	cr
CR	CCRR RED	CCRr RED	CcRR RED	CcRr RED
Cr	CCRr RED	CCrr WHITE	CcRr RED	Ccrr WHITE
cR	CcRR RED	CcRr RED	ccRR WHITE	ccRr WHITE
cr	CcRr RED	Ccrr WHITE	ccRr WHITE	ccrr WHITE

Fig. 7.3. Diagram showing the expected composition of the F_2 from the interaction of genes C and R in sweet peas, giving 9 : 7 ratio

flowered plants has the genotype $CCcc$ and the $RRrr$. The offspring of their cross $CcRr$ will develop the red colour because both the dominant C and R are present together. This F_1 offspring will form four kinds of gametes *viz.* CR, Cr, cR and cr. The result of a cross between two F_1 plants is shown in figure 7.3. There are nine F_2 plants which have both C and R. These are, therefore, red, the other seven have either C or R alone and are white. This explains the 9 : 7 ratio which is obviously a modified dihybrid ratio (9 : 3 : 3 : 1) in which the last three classes are phenotypically indistinguishable (all being white) from one another.

Similar cases are met with in Indian crop plants. In rice, for example, there are two grey grained races which, when crossed produced F_1 hybrid with red grains. The original grain colour in

rice was red. Each grey race is due to a recessive mutation, and the two mutations are in separate chromosomes. The mutant genes may be designated pr_1 and pr_2 and their normal alleles by Pr_1 and Pr_2. The genotypes of the two pure grey grained varieties will be $Pr_1Pr_1pr_2pr_2$ and $pr_1pr_1Pr_2Pr_2$. They are grey grained because each of the recessive gene interferes with the development of the normal colour. The two dominant genes are both necessary for the red colour. They must be present together, if red colour is to develop. A cross of the two grey races ($Pr_1Pr_1pr_2pr_2 \times pr_1pr_1Pr_2Pr_2$) produces F_1 of genotype $Pr_1pr_1Pr_2pr_2$. These are red grained because both the dominant genes Pr_1 and Pr_2 are present. The F_1 produce gametes of four classes (Pr_1Pr_2, Pr_1pr_2, pr_1Pr_2, pr_1pr_2) and when the F_1 are self-fertilised they produce the F_2 phenotype ratio of 9 red : 7 grey. This may be verified by filling up the checkerboard, reading off the phenotypes and gathering together all F_2 combinations of like appearance.

In millets, two white-grained races when crossed produce F_1 hybrids that are brown-grained. The F_2 consist of brown and white types in the ratio of 9 : 7.

When two genes interact in this way to produce a character different from the one which each produces when alone, they are called **complementary**. The combination of complementary genes also explains the so-called phenomenon of '**throwback**' or **reversion** to an ancestral type. Similar inheritance occurs in animals and probably also in man. It appears, although there is no definite evidence, that traits like exceptional musical talent or high intelligence result from the interaction of complementary genes, each coming from a different parent. This might explain the fact that sometimes outstanding ability appears in one member of a family where other children and the parents are not outstanding.

4. **Supplementary factors (9 : 3 : 4 ratio).** Supplementary genes are two independent pairs which interact in such a way that one dominant will produce its effect whether the other is present or not but the second can produce its effect only in the presence of the first. The coat colour of rats and other rodents varies a good deal and is inherited as a Mendelian trait. The black colour (due to a gene C) is dominant over albino (lack of pigment, c). Besides, there is the wild type whose coat colour is agouti or grey. In this, the individual hairs are black at the base with a yellow band near the tip, beyond which again the hair tip is intense black. The mass effect of such a coat is to produce a neutral grey. This in-

conspicuous and hence protective colour pattern, which is characteristic of wild rodents is due to a dominant gene *A*. The gene *A* turns black fur into agouti. A black rat, then, is always homozygous for recessive allele *aa*, in addition to having at least one dominant *C*. But neither *A* nor *a* has any effect in the absence of *C*; the albino rats, therefore, may or may not carry the gene *A*. When a true breeding black rat is crossed with an albino carrying the dominant gene *A*, all the F_1 offspring are of agouti type. It is clear that the agouti factor could not have been brought into the F_1 rats through the black parent, for then they would be agouti and not black. It must have come through the albino rat, on which

P generation	CCaa Black		ccAA Albino
Gametes of *P*	Ca	×	cA
F_1 generation		CcAa Agouti	

Sperms of F_1

Eggs of F_1	CA	Ca	cA	ca
CA	CCAA Agouti	CCAa Agouti	CcAA Agouti	CcAa Agouti
Ca	CCAa Agouti	CCaa Black	CcAa Agouti	Ccaa Black
cA	CcAA Agouti	CcAa Agouti	ccAA Albino	ccAa Albino
ca	CcAa Agouti	Ccaa Black	ccAa Albino	ccaa Albino

Fig. 7.4. F_2 generation of a cross between black and albino rats which produce all agouti offspring in F_1 (9 : 3 : 4 ratio)

the agouti factor has no effect. The genotypes of the two parents and the F_1 offspring must be as given in figure 7.4.

P generation	Black purple PPqq		Brown ppQQ
Gametes of *P*	Pq	×	pQ
F_1		Red purple PpQq	

Pollen of F_1

Ovules of F_1 (F_2)	PQ	Pq	pQ	pq
PQ	PPQQ Red purple	PPQq Red purple	PpQQ Red purple	PpQq Red purple
Pq	PPQq Red purple	PPqq Black purple	PpQq Red purple	Ppqq Black purple
pQ	PpQQ Red purple	PpQq Red purple	ppQQ Brown	ppQq Brown
pq	PpQq Red purple	Ppqq Black purple	ppQq Brown	ppqq Brown

Fig. 7.5. Inheritance of glume colour in millet.

When the F_1 offspring are mated with each other, the F_1 and the original parental types appear in the F_2 generation in the ratio of 9 agouti : 3 black : 4 albino. The genotypes of the F_1 gametes and F_2 generation are given in figure 7.4.

Nine of the zygotes in the checkerboard have at least one *A* and one *C* factor and are, therefore, agouti ; three of them have at least one *C* factor but lack *A* and are, therefore, black ; four of them lack

the factor *C* and are, therefore, albino. The interaction of the two factors explains the 9 : 3 : 4 ratio which is a modified 9 : 3 : 3 : 1 ratio in which the last two classes are superficially alike.

The 9 : 3 : 4 ratio is also shown by the glume colour in millet and is due to the interaction of two dominant factors *P* and *Q*. The black purple colour (*P*) is dominant over brown (*p*). The factor *Q* borne on another chromosome has no effect by itself or in the presence of the recessive factor *p*. The recessive factor *q* also is without any phenotypic effect. In the last two cases the glume colour remains brown. But when *P* and *Q* are together the black purple colour is changed to red. Thus, when a true breeding black purple (*PPqq*) is crossed to a brown variety carrying the *Q* factor the F_1 plants are red glumed. The F_2 consists of 9 red purple : 3 black purple : 4 brown. The phenotypes and genotypes of such a cross are given in figure 7.5. In lab-lab, Khaki seedcoat colour is dominant over buff. The F_2 of this cross gives 9 Chocolates : 3 Khaki : 4 Buff.

Green-fruited=*wwyy*
Yellow-fruited=*wwYY*
White-fruited=*WWYY* or *WWyy*

	WY	Wy	wY	wy
WY	WWYY White	WWYy White	WwYY White	WwYy White
Wy	WWYy White	WWyy White	WwYy White	Wwyy White
wY	WwYY White	WwYy White	wwYY Yellow	wwYy Yellow
wy	WwYy White	Wwyy White	wwYy Yellow	wwyy Green

Fig. 7.6. F_2 generation of a cross between white-fruited squash plant which carries yellow, with a green-fruited one (12 : 3 : 1 ratio)

5. **Epistasis (12 : 3 : 1 ratio).** Sometimes two independent genes (not members of an allelic pair) affect the same trait in an organism. One gene masks the effect of the other. This effet is known as **epistasis** in contrast to dominance which concerns two alleles of the same gene. The gene that masks the effect of another is said to be **epistatic** and the gene whose expression is prevented is said to be **hypostatic.**

In squash, *Cucurbita pepo*, the yellow fruit colour due to a gene *Y* is dominant to green, which is due to its absence. Another gene *W* produces a white colour and is epistatic to (masks) the gene *Y*. When *W* is present the fruit colour will always be white irrespective of the presence of other colour genes. In the absence of *W*, the fruit colour will be yellow or green, according as *Y* is present or absent. The genotypes of the true breeding green, yellow and white-fruited plants will be as under :

When a white variety with the genotype *WWYY* is crossed with a green variety (*wwyy*), the F_1 offspring is white-fruited (*WwYy*). In the F_2 generation appear three kinds of plants, white, yellow, and green in the ratio of 12 : 3 : 1. The F_1 hybrid produces four kinds of gametes, *WY*, *Wy*, *wY* and *wy*. The result of their chance union is shown in figure 7.6. Out of the 16 zygotes, 12 carry at least one gene *W* and will, therefore, be white, 3 carry at least one *Y* but no *W* and will, therefore, be yellow, 1 carries neither *W* nor *Y* and will be green. This explains the 12 : 3 : 1 ratio, which is actually obtained in breeding experiments.

An example of similar type is met with in the grain colour of cholam (*Sorghum caudatum*). Two gene pairs *Z-z* and *W-w* interact to produce the grain colour. Gene *Z*, which gives pearly grains, is dominant over *z* which gives chalky grains. The pearly grains are shining, oily, white and translucent; the chalky grains are lustreless, opaque and salt white. The gene *W* for red grain colour is dominant over *w* which gives white colour. *W* is also dominant (epistatic) to *Z* and masks the effect of the latter. When *W* is present, the grain colour is red and it is not possible to know whether the grains are pearly or chalky. In its absence the appearance of the grain will be pearly or chalky according as *Z* is present or absent. Thus, when a pure red-grained type with the genotype *WWZZ* is crossed with the chalky variety *wwzz* or when a red-grained type with the genotype *WWzz* is crossed with the pearly variety *wwZZ*, the F_1 offspring are red-grained (*WwZz*). The F_1 will produce four kinds of gametes : *WZ*, *Wz*, *wZ* and *wz*. The F_2 will consist of 12 red :

3 pearly white : 1 chalky as shown in figure 7.7.

	WZ	Wz	wZ	wz
WZ	WWZZ Red	WWZz Red	WwZZ Red	WwZz Red
Wz	WWZz Red	WWzz Red	WwZz Red	Wwzz Red
wZ	WwZZ Red	WwZz Red	wwZZ Pearly	wwZz Pearly
wz	WwZz Red	Wwzz Red	wwZz Pearly	wwzz Chalky

Fig. 7.7. Epistatic inheritance of grain colour in cholam

The 12 red types are really made up of 9 red pearly and 3 red chalky, but the pearly and chalky characters are not visible because they are masked by red, being hypostatic to it.

In millet (*Sorghum vulgare*) yellow grain colour is epistatic to pearly and chalky and the F_2 gives 12 yellow : 3 white pearly : 1 white chalky.

6. **Inhibitory factors. 13 : 3 ratio.** An inhibitory factor is one which by itself has no phenotypic effect but when present in the dominant form prevents or inhibits the expression of another independent dominant present in another chromosome. This may be illustrated by the inheritance of leaf colour in rice. Here purple pigment (*Lp*) is a monogenic dominant to green (*lp*). There is another factor (*I*) which inhibits the effect of *Lp* and the leaves become green. The inhibitory factor has no effect in the recessive form (*i*) so that the leaves will be purple or green according as *Lp* is present or not.

In this case, a cross between a green and a purple variety gives an F_2 ratio of 13 green : 3 purple. The theoretical results to be expected from such a cross are given in figure 7.8.

P generation	Purple iiLpLp		Green IIlplp
Gametes of *P*	iLp	×	Ilp
F_1		Green IiLplp	

Pollen of F_1

Ovules of F_1	ILp	Ilp	iLp	ilp
ILP	IILpLp Green	IILplp Green	IiLpLp Green	IiLplp Green
Ilp	IILplp Green	IIlplp Green	IiLplp Green	Iilplp Green
iLp	IiLpLp Green	IiLplp Green	iiLpLp Purple	iiLplp Purple
ilp	IiLplp Green	Iilplp Green	iiLplp Purple	iilplp Green

Fig 7.8. Inheritance of leaf colour in rice, showing the effect of inhibiting factors

7. **Duplicate factors (15 : 1 ratio).** Another type of gene interaction is that in which two or more genes in different chromosome pairs have an identical effect on a trait. These are called **duplicate factors or duplicate genes.** An example is the inheritance of endosperm colour in maize. Pure yellow × white cross in this case yields F_1 seeds with yellow endosperm. Yellow is thus dominant. The F_1 plants on self-pollination give an F_2 generation of 15 yellow : 1 white. The fact that the white variety accounts for only one-sixteenth of the F_2 progeny at once suggests that the case is of a dihybrid cross and not a monohybrid one. Yellow endosperm is due to two independent dominant genes, say Y_1 and Y_2.

P generation	$Y_1Y_1Y_2Y_2$ Yellow		$y_1y_1y_2y_2$ White
Gametes of *P*	Y_1Y_2	×	y_1y_2
F_1		$Y_1y_1Y_2y_2$ Yellow	

Pollen of F_1

Ovules of F_1 (F_2)	Y_1Y_2	Y_1y_2	y_1Y_2	y_1y_2
Y_1Y_2	$Y_1Y_1Y_2Y_2$ Yellow	$Y_1Y_1Y_2y_2$ Yellow	$Y_1y_1Y_2Y_2$ Yellow	$Y_1y_1Y_2y_2$ Yellow
Y_1y_2	$Y_1Y_1Y_2y_2$ Yellow	$Y_1Y_1y_2y_2$ Yellow	$Y_1y_1Y_2y_2$ Yellow	$Y_1y_1y_2y_2$ Yellow
y_1y_2	$Y_1y_1Y_2Y_2$ Yellow	$Y_1y_1Y_2y_2$ Yellow	$y_1y_1Y_2Y_2$ Yellow	$y_1y_1Y_2y_2$ Yellow
y_1X_2	$Y_1y_1Y_2y_2$ Yellow	$Y_1y_1y_2y_2$ Yellow	$y_1y_1Y_2y_2$ Yellow	$y_1y_1y_2y_2$ White

Fig. 7.9 Inheritance of endosperm colour in maize due to duplicate factors (15 : 1 ratio)

The presence of either or both genes causes yellow endosperm, while in the absence of both, white endosperm is produced. The homozygous yellow parent has the genotype $Y_1Y_1Y_2Y_2$ and the recessive parent $y_1y_1y_2y_2$. The result of the dihybrid cross is shown in figure 7.9. It will be clear that out of every sixteen offspring in the F_2 generation, fifteen have at least one of the dominant genes, so that they will all have the yellow endosperm ; one is a double recessive and will have white endosperm. This explains the 15 : 1 ratio obtained in breeding experiments. This ratio is only a modified 9 : 3 : 3 : 1 ratio in which the first three classes have the same phenotype.

A similar case is the inheritance of 'awned-awnless' grain in rice. Awned × awnless cross in this case gives F_1 awned grains and the F_2 consisted of 15 awned : 1 awnless. Obviously, two factor pairs are involved, A_1 and A_2 (awned) being dominant over a_1 and a_2 respectively (awnless). The genotypes of this cross are given in figure 7.10. Let the students themselves determine the F_2 phenotypic and genotypic ratio by the checkerboard method.

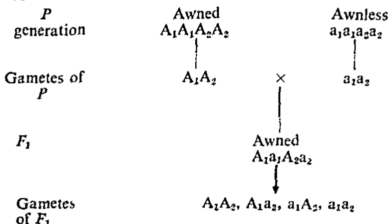


Fig. 7.10. Inheritance of awned and awnless characters of grain in rice due to duplicate factors

The 15 : 1 ratio may be easily calculated by making a checkerboard as usual. In ragi, chlorophyll inheritance is due to duplicate pairs of factors C_1–c_1 and C_2–c_2. The F_2 of such a cross gives 15 green : 1 albino seedling.

8. **Polymerism. 9 : 6 : 1 ratio.** This is the case of independent dominant factors which resemble duplicate factors in that when only one of them is present (A or B), the phenotypic effect is the same but when both are present together ($A+B$), at least in a single dose the phenotypic effect is intensified. An instance of this type is found in the inheritance of fruit shape in pumpkin (*Cucurbita pepo*). Here spherical fruit shape is dominant over cylindrical and is due to two independent factors S_1 and S_2. When two different spherical races were crossed the F_1 was disc-shaped and the F_2 gave 9 disc : 6 sphere : 1 cylindrical. The mode of inheritance in this and case is given in figure 7.11.

9 zygotes in the checkerboard have at least one S_1 and one S_2 and are disc types ; 6 of them have only S_1 (at least one) or only S_2 are spheres ; 1 has neither S_1 nor S_2 and is cylindrical.

The inheritance of pericarp colour in wheat follows the same pattern. Here two factors for red colour C_1 and C_2 are involved.

P generation	$Y_1Y_1Y_2Y_2$ Yellow		$y_1y_1y_2y_2$ White
Gametes of *P*	Y_1Y_2	×	y_1y_2
F_1		$Y_1y_1Y_2y_2$ Yellow	

Pollen of F_1

F_2

Ovules of F_1	Y_1Y_2	Y_1y_2	y_1Y_2	y_1y_2
Y_1Y_2	$Y_1Y_1Y_2Y_2$ Yellow	$Y_1Y_1Y_2y_2$ Yellow	$Y_1y_1Y_2Y_2$ Yellow	$Y_1y_1Y_2y_2$ Yellow
Y_1y_2	$Y_1Y_1Y_2y_2$ Yellow	$Y_1Y_1y_2y_2$ Yellow	$Y_1y_1Y_2y_2$ Yellow	$Y_1y_1y_2y_2$ Yellow
y_1Y_2	$Y_1y_1Y_2Y_2$ Yellow	$Y_1y_1Y_2y_2$ Yellow	$y_1y_1Y_2Y_2$ Yellow	$y_1y_1Y_2y_2$ Yellow
y_1y_2	$Y_1y_1Y_2y_2$ Yellow	$Y_1y_1y_2y_2$ Yellow	$y_1y_1Y_2y_2$ Yellow	$y_1y_1y_2y_2$ White

Fig. 7.9. Inheritance of endosperm colour in maize due to duplicate factors (15 : 1 ratio)

The presence of either or both genes causes yellow endosperm, while in the absence of both, white endosperm is produced. The homozygous yellow parent has the genotype $Y_1Y_1Y_2Y_2$ and the recessive parent $y_1y_1y_2y_2$. The result of the dihybrid cross is shown in figure 7.9. It will be clear that out of every sixteen offspring in the F_2 generation, fifteen have at least one of the dominant genes, so that they will all have the yellow endosperm ; one is a double recessive and will have white endosperm. This explains the 15 . 1 ratio obtained in breeding experiments. This ratio is only a modified 9 : 3 : 3 : 1 ratio in which the first three classes have the same phenotype.

A similar case is the inheritance of 'awned-awnless' grain in rice. Awned × awnless cross in this case gives F_1 awned grains and the F_2 consisted of 15 awned : 1 awnless. Obviously, two factor pairs are involved, A_1 and A_2 (awned) being dominant over a_1 and a_2 respectively (awnless). The genotypes of this cross are given in figure 7.10. Let the students themselves determine the F_2 phenotypic and genotypic ratio by the checkerboard method.

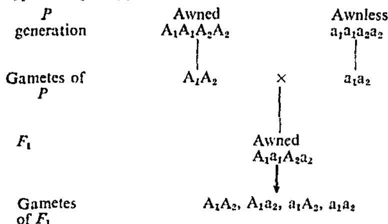


Fig. 7.10. Inheritance of awned and awnless characters of grain in rice due to duplicate factors

The 15 : 1 ratio may be easily calculated by making a checkerboard as usual. In ragi, chlorophyll inheritance is due to duplicate pairs of factors C_1–c_1 and C_2–c_2. The F_2 of such a cross gives 15 green : 1 albino seedling.

8. **Polymerism. 9 : 6 : 1 ratio.** This is the case of independent dominant factors which resemble duplicate factors in that when only one of them is present (A or B), the phenotypic effect is the same but when both are present together (A+B), at least in a single dose the phenotypic effect is intensified. An instance of this type is found in the inheritance of fruit shape in pumpkin (*Cucurbita pepo*). Here spherical fruit shape is dominant over cylindrical and is due to two independent factors S_1 and S_2. When two different spherical races were crossed the F_1 was disc-shaped and the F_2 gave 9 disc : 6 sphere : 1 cylindrical. The mode of inheritance in this and case is given in figure 7.11.

9 zygotes in the checkerboard have at least one S_1 and one S_2 and are disc types ; 6 of them have only S_1 (at least one) or only S_2 are spheres ; 1 has neither S_1 nor S_2 and is cylindrical.

The inheritance of pericarp colour in wheat follows the same pattern. Here two factors for red colour C_1 and C_2 are involved.

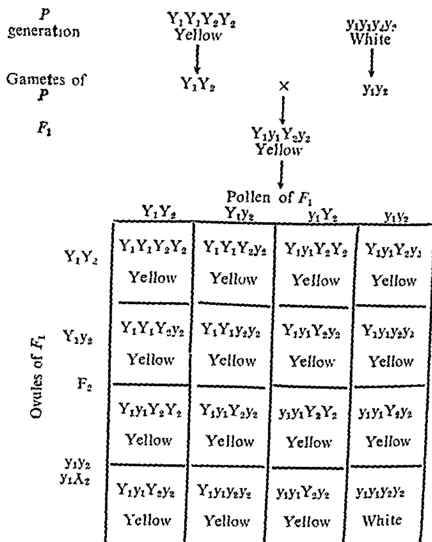


Fig. 7.9. Inheritance of endosperm colour in maize due to duplicate factors (15 : 1 ratio)

The presence of either or both genes causes yellow endosperm, while in the absence of both, white endosperm is produced. The homozygous yellow parent has the genotype $Y_1Y_1Y_2Y_2$ and the recessive parent $y_1y_1y_2y_2$. The result of the dihybrid cross is shown in figure 7.9. It will be clear that out of every sixteen offspring in the F_2 generation, *fifteen have at least one of the dominant genes, so that they will all have the yellow endosperm ; one is a double recessive and will have white endosperm. This explains the* 15 : 1 *ratio obtained in breeding experiments. This ratio is only a modified* 9 : 3 : 3 : 1 *ratio in which the first three classes have the same* phenotype.

A similar case is the inheritance of 'awned-awnless' grain in rice. Awned × awnless cross in this case gives F_1 awned grains and the F_2 consisted of 15 awned : 1 awnless. Obviously, two factor pairs are involved, A_1 and A_2 (awned) being dominant over a_1 and a_2 respectively (awnless). The genotypes of this cross are given in figure 7.10. Let the students themselves determine the F_2 phenotypic and genotypic ratio by the checkerboard method.

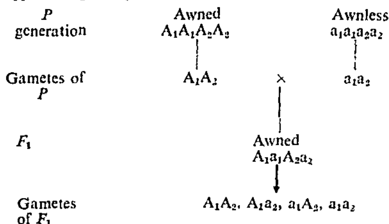


Fig. 7.10. Inheritance of awned and awnless characters of grain in rice due to duplicate factors

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9 zygotes in the checkerboard have at least one S_1 and one S_2 and are disc types ; 6 of them have only S_1 (at least one) or only S_2 are spheres ; 1 has neither S_1 nor S_2 and is cylindrical.

The inheritance of pericarp colour in wheat follows the same pattern. Here two factors for red colour C_1 and C_2 are involved.

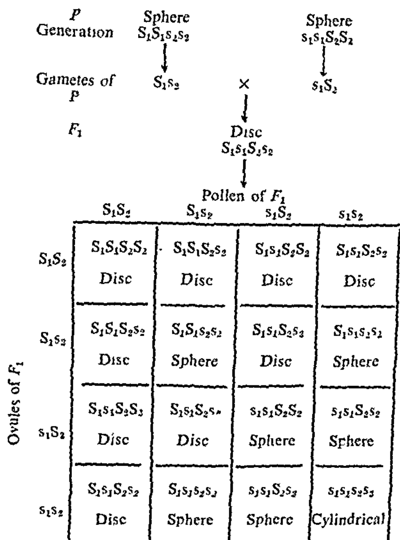


Fig. 7.11. Inheritance of fruit shape in pumpkin due to polymeric factors

When both the dominants are present the grain colour is deep red; when only one of the two dominants is present the grain colour is light red; and when both the dominants are absent the grain colour is white. A deep red × white cross gives deep red F_1 off-spring and the F_2 gives 9 deep red : 6 light red : 1 white. The mode of inheritance is explained in figure 7.12. Nine F_2 zygotes have both the factors C_1 and C_2 and are deep red; 6 of them have either only C_1 or only C_2 and are light red; 1 has neither C_1 nor C_2 and is white.

9. *Multiple genes or polygenes—Quantitative Inheritance.* The characters, whose inheritance we have studied in the preceding

P Generation — Deep red $C_1C_1C_2C_2$ — White $c_1c_1c_2c_2$

Gametes of *P* — C_1C_2 × c_1c_2

F_1 — Deep Red $C_1c_1C_2c_2$

Pollen of F_1

Ovules of F_1 (F_2)	C_1C_2	C_1c_2	c_1C_2	c_1c_2
C_1C_2	$C_1C_1C_2C_2$ Deep red	$C_1C_1C_2c_2$ Deep red	$C_1c_1C_2C_2$ Deep red	$C_1c_1C_2c_2$ Deep red
C_1c_2	$C_1C_1C_2c_2$ Deep red	$C_1C_1c_2c_2$ Light red	$C_1c_1C_2c_2$ Deep red	$C_1c_1c_2c_2$ Light red
c_1C_2	$C_1c_1C_2C_2$ Deep red	$C_1c_1C_2c_2$ Deep red	$c_1c_1C_2C_2$ Light red	$c_1c_1C_2c_2$ Light red
c_1c_1	$C_1c_1C_2c_2$ Deep red	$C_1c_1c_2c_2$ Light red	$c_1c_1C_2c_2$ Light red	$c_1c_1c_2c_2$ White

Fig. 7.12. Inheritance of pericarp colour in wheat grain due to two polymeric factors

pages are such as can be easily distinguished into sharply defined and well cut alternative phenotypes. In peas, for example, the characters tall and dwarf plants, smooth and wrinkled seeds, yellow and green pods, are such that a casual look is enough to classify the plants into easily recognisable alternative groups. The traits show complete dominance and between the two extremes of a character there are no intermediates. Such characters are referred to as qualitative characters. Many characters of agro-*nomic importance, for example rough and smooth* awns, rust-resistance and rust susceptibility, are of this type. In most cases

of this type, the two alternative characters are controlled by a single gene pair.

The traits influenced by duplicate factors are also of this type. Here the individual will show the effect if one or more genes are present The effect is the same whether only one gene is present or more. The effect of the genes is only qualitative. It is a question of having a gene (or more) or not having it. The number of genes makes no difference.

There are many characters in plants and animals whose inheritance does not conform to this pattern. There are cases in which a character is not sharply differentiated into well defined extremes but shows a continuous variation between the two extremes. A case of this type came to the notice of the famous plant breeder Kolreuter. He crossed a dwarf variety of tobacco with a tall variety. The F_1 were intermediate between the two parents. There was no dominance. The F_2 progeny contained a few dwarf and some talls but the great majority showed a wide range of variation between these two extremes. Kolreuter was unable to explain these results.

There are a large number of economically important traits, which are of interest to geneticists and plant breeders, that show a wide range of variation from one extreme to the other. There is, in such cases, a continuous gradation of variability. Such traits as height, weight and size of grain, yield, number of seeds in a fruit or number of grains in an ear of wheat, length of ears, number of rows of kernels in maize, time taken to reach maturity, winter hardiness, resistance to lodging, drought-resistance and protein content of wheat belong to this category. Because these characters can be expressed in terms of units of length, weight, time, numbers etc., they are described as **quantitative characters**. Milk production in cows and egg-laying in chickens also *belong to this category of hereditary traits. It will be evident that the* variation in quantitative characters is of a *continuous type* as compared to the discontinuous variation of qualitative characters. Moreover, environment has a greater influence on the quantitative characters than on the qualitative characters.

The inheritance of quantitative characters has been explained by assuming that they *are influenced* by a number of independent genes, each gene having a small and similar effect, and the effect of several genes is additive. In such cases, the net effect on the trait will depend upon the number of genes present. Thus, one

gene will have a positive effect, two genes will have a greater effect and total effect of three genes will be still greater, and so on. The effect adds up with each increase in the number of genes so that it is said to be cumulative. Such genes are described as **multiple genes** or **polygenes** and the traits influenced by them are described as **polygenic**. This concept of quantitative inheritance is called **multiple gene hypothesis**. It was first suggested by Yule (1906) and elaborated by Nilsson-Ehle (1908) and East (1916).

A classical example of the interaction of multiple factors is the inheritance of kernel colour in wheat studied by the Swedish geneticist and plant breeder Nilsson-Ehle in 1908. In crosses between a red-kerneled variety and a white-kerneled variety the F_1 seeds had a red colour intermediate between the two parents. The F_2 *generation gave a ratio of 15 reds : 1 white but all the reds were* not of uniform colour. Some of them had about the same shade as the F_1, some were paler, others had a stronger red colour and a few were dark-red like the red grandparents. The F_2 progeny showed a continuous gradation from white to red. These results were similar to those obtained by Kolreuter in his experiments with tobacco. As each of the original parental colours of wheat kernel appeared *in 1/16th of the* F_2 *progeny it was assumed that* there are two independent pairs of genes R_1 and R_2 for red and that the four members of these pairs are cumulative in their effect. The results of the cross are shown in figure 7.13.

The F_2 generation may be classified into the following five classes :

1/16ths have 4 dominant genes for red colour and are dark red.
4/16ths „ 3 „ „ „ „ „ and are a little lighter.
6/16ths „ 2 „ „ „ „ „ and are intermediate.
4/16ths „ 1 dominant gene for red colour „ are paler.
1/16ths „ no „ „ „ „ „ „ are white.

Sometimes, in the progeny may appear individuals which show greater intensity of a character than was present in the parents. This happens when the parents possess combined genotypes, *i.e. they are heterozygotes of varying degree and do not represent the* two extreme homozygous condition. Thus, if two medium red varieties of wheat, with the genotypes $R_1R_1r_2r_2$ and $r_1r_1R_2R_2$, are crossed the F_1 hybrids will have medium red kernels, with the genotype $R_1r_1R_2r_2$ like the F_1 hybrid in figure 7.13. The F_2 progeny will produce some individuals in which the kernel colour will be darker (with 3 and 4 dominant genes) and others in which

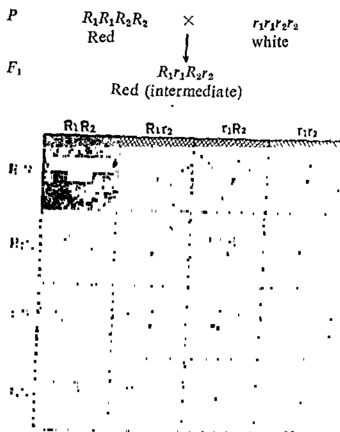


Fig. 7.13. Diagram showing the result of a cross between a red kerneled and a white kerneled wheat, where the red colour is due to the operation of two cumulative genes R_1 and R_2. The different shades of red colour have been indicated by differences in cross hatching

the kernel colour will be lighter (with one or no dominant genes) than the parents. Such offspring arise as a result of segregation and recombination which bring together a larger number of genes in the offspring than were present in the parents. They are called *transgressive segregants.* The *plant breeders employ this method* to produce varieties which are superior to the parental types *in* quantitative traits. Consider, for example, a cross between two *high* yielding varieties, each of which possesses a different combination of genes for yielding ability. Selection in the *progeny may* bring out types in which combination of genes for yielding ability may be better than in either parent.

Still other crosses gave an F_2 ratio of 63 : 1 between the reds and whites. Evidently, three independent genes pairs for red R_1R_1, R_2R_2 and R_3R_3 with similar but cumulative effect are con-

cerned here. The range in the intensity of the red colour was even greater. This is but to be expected because the number of genes for red colour in the various individuals would vary from one to six.

We may illustrate the phenomenon of polygenic inheritance by another example concerning the inheritance of ear length in maize investigated by Emerson and East. When a small eared variety with an average ear length of 6·6 cm. was crossed with a long eared variety with an average length of 16·8 cm. the F_1 progeny had intermediate ear length with an average of 12·1 cm. The F_2 showed a continuous variation ranging from the small extreme to the long one. The parental types each accounted for 1/16 of the total F_2 progeny. It is obvious that two gene pairs for ear length were involved. Between themselves they contributed 10·2 cm. (16·8—6·6) to the residual ear length. The contribution of each gene is, therefore, 2·55 cm. (10·2/4).

In the examples of inheritance described above, two or three gene pairs are involved. More often, agronomically valuable traits that exhibit quantitative inheritance are influenced by more gene pairs than are involved here.

Some interesting human traits also are controlled by polygenes. Skin-colour and intelligence in man are of this type. The inheritance of human skin colour seems to follow a similar pattern. Marriages between black Negroes and white-skinned Caucasians result in offspring which are more or less intermediate between the parents. Davenport explained the difference in pigment between Negro and Caucasian people by assuming that it is due to two gene pairs which do not show dominance but are cumulative. A "pure Negro" would have the pigment genes $P_1P_1P_2P_2$ and, therefore, his colour value would be very dark. By contrast, a pure white would have only non-pigment genes, $p_1p_1p_2p_2$ and his skin will be very light. A marriage between a Negro and a white would give F_1 offspring with the genotype $P_1p_1P_2p_2$. With two pigment genes these would be mulattos. Their colour value would be 50, intermediate between the two parents. Intermarriages among mulattos can produce offspring (F_2) showing wide variation in skin colours due to variation in the number of pigment genes passed on to them by the two parents. The genotypes and phenotypes of the F_2 which may be expected from such intermarriages are illustrated in figure 7.14.

Parents	Black $P_1P_1P_2P_2$	×	White $p_1p_1p_2p_2$
F_1		Mulattos $P_1p_1P_2p_2$	
	Mulatto $P_1P_1P_2p_2$	×	Mulatto $P_1p_1P_2p_2$

Phenotype	Genotype	Genotypic ratio	Phenotypic ratio
Black	$P_1P_1P_2P_2$	1	1
Dark	$P_1p_1P_2P_2$	2	4
	$P_1P_1P_2p_2$	2	
Intermediate	$P_1p_1P_2p_2$	4	6
	$P_1P_1p_2p_2$	1	
	$p_1p_1P_2P_2$	1	
Light	$P_1p_1p_2p_2$	2	4
	$p_1p_1P_2p_2$	2	
White	$p_1p_1p_2p_2$	1	1

Fig. 7.14. Result of intermarriages between Negroes and white people and between mulattos, based on the assumption that two pairs of pigment genes are involved

Most probably, more than two gene pairs are involved in the inheritance of skin colour in man. According to Gates there are three pairs of such cumulative genes while Stern thinks that 4, 5, and 6 gene pairs would explain better the observed statistics. The question of number of gene pairs involved is complicated by the profound modifying effect that environmental factors like sun and wind, and the use of cosmetics and beautifying treatments, have on pigmentation. A further complication arises from the probability that some genes act as basic colour genes, others as activators and others as modifiers. To cite an instance, there seems to be a modifying gene which inhibits all pigment production, regardless of what colour genes may be present. This inhibitor may cause a condition known as albinism in which the skin, the hair and the eyes are colourless.

Height in man is also a polygenic character, being inherited by a much more complex set of multiple factors, possibly 10 or more pairs of genes being involved. Tallness is recessive to shortness. Larger the number of dominants, shorter the individual. Because of many pairs of genes and because height is modified by environmental conditions, we do not have the alternative conditions, short versus tall, or even short, medium and tall. Instead, there are people of every height from 55 inches to about 84 inches.

ISOALLELS

Sometimes, a dominant gene occurs in two or more forms. In homozygous condition these multiple dominant alleles will produce the same phenotypic effect but in the heterozygous state (that is in combination with a recessive allele) their effect will show a small difference. Thus, in Drosophila, the gene for red eye colour is dominant over white. In the homozygous condition they will produce dark red colour. But in combination with the white allele the gene for red colour produces a dark red colour in flies from Soviet Russia but the same combination in the flies coming from the U.S.A. produces a light red colour. This means that the dominant gene for red colour occurs in two forms. These are called isoalleles.

PSEUDOALLELES

Alleles are different forms of the same gene situated at the same locus. Sometimes, it so happens that genes that are situated at adjacent but different loci affect the same character in a related manner as if they are different forms (alleles) of the same gene. They are called Pseudoalleles. These closely linked pseudoalleles, unlike the alleles, show recombinations by crossing over.

PHENOCOPY

Characters are the result of interaction between the genes and the environment. When a gene mutates, its phenotypic effect also changes. Sometimes, a change in the environment produces a phenotypic effect of the normal gene which resembles the effect of an already known mutant. The effect of the normal gene under the changed environment is an imitation (mimic) of the mutant gene. Such an imitation induced by environmental changes has been

termed by Goldschmidt as phenocopy. In fowls, a mutant gene is responsible for the character, rumplessness, in which the caudal vertebrae and tail feathers do not develop. Rumplessness is also induced as a phenocopy when normal eggs, that is those which do not have the gene for rumplessness, are treated with insulin before incubation. Phenocopies of other mutant genes are also produced in Drosophila by high temperature treatment of the larvae for short periods. Sometimes, different (non-allelic) genes can produce the same phenotype. This phenomenon is called genocopy or genetic mimic.

PENETRANCE AND EXPRESSIVITY

Ordinarily, a recessive gene produces its phenotypic effect when in the homozygous condition and a dominant gene produces its effect whether it is homozygous or heterozygous. Some genes fail to produce their phenotypic effects when they should. The ability of a gene to produce its effect is called **penetrance**. A gene that always produces the expected effect is said to have 100 per cent penetrance. If its phenotypic effect is produced only in 80 per cent of the individuals that possess it then it is said to show 80 per cent penetrance. The percentage of penetrance can be altered by changing the environmental conditions such as temperature, moisture, etc. In cotton, a mutant gene produces crinkled leaf. While all the leaves produced in the normal season are crinkled some of the leaves produced late in the season do not show this character and are normal. This means that penetrance is zero or that the gene is non-penetrant. Penetrance is an all-or-none phenomenon. Either the gene produces its effect in an individual or not at all.

Sometimes there is great variation in the manner in which a character is expressed in different plants. In the venturra variety of Lima beans, a dominant gene is responsible for the tips and margins of the leaves of the seedlings to be partially deficient in chlorophyll. Sometimes only the tips are affected and sometimes only the margins. In other words, this single gene can express itself in a variety of ways that may resemble a number of characters. This gene is then said to show variable **expressivity**. Whether a gene is expressed at all is denoted by the term penetrance whereas the term expressivity denotes the manner or degree of its expression.

XENIA AND METAXENIA

The monocotyledonous seeds, like those of cereals, contain a special food storage tissue outside the embryo. This is called the endosperm. The embryo is formed by the union of a male gamete, introduced by the pollen-grain, with the egg nucleus and the endosperm is formed as a result of the process of double fertilization in which the second male gamete fuses with, the two polar nuclei (triple fusion) giving rise to a triploid fusion nucleus. In cross fertilized plants, the embryo and the endosperm are hybrids while the fruit and seedcoats are the maternal tissues The effect of cross-pollination on the embryo will become evident when the new generation is raised from the seeds but its effect on the endosperm will be immediately visible in the seed. The immediate effect of foreign pollen on visible characters of the endosperm is called **xenia**. This has been best studied in maize plant An example of this is the endosperm colour. If a white-endosperm variety is open pollinated in the field where there are also plants of the yellow endosperm variety then the cobs that develop will contain a mixture of yellow and white seeds. The yellow colour of the endosperm in the yellow seeds is the result of fertilization by pollen from the yellow variety. The yellow colour indicates that the seeds are hybrids and the white seeds are homozygous. The yellow colour of the endosperm is dominant over white and when the plants raised from the yellow seeds are self-pollinated, yellow and white seeds are produced in the ratio of 3 : 1. Another example of xenia effect may be cited. If a sweet corn (maize) variety is pollinated by a starchy variety, the endosperm is starchy because the starchy gene introduced by the pollen is dominant over its sugary allele.

Xenia has also been observed in rice. When a glutinous variety is fertilized by pollen from a starchy variety, the F_1 grains are starchy (dominant). The F_1 hybrids on self-pollination segregate to produce 3 starchy : 1 glutinous grains. In pearl millet (*Pennisetum typhoides*), the common colour of the endosperm is iron-grey. When it is crossed with the yellow-grained *P. leonis* the grains are yellow-coloured (dominant).

Often several pollen tubes, one from each pollen-grain, [illegible] down the style simultaneously. In such cases there is some [illegible] that a male gamete from one pollen tube may fertilize the [illegible] a male gamete from another pollen tube may [illegible] nuclei. This phenomenon, which it called hetero[illegible]

sometimes lead to different genotypes of the endosperm and the embryo. Cases are known where the endosperm is heterozygous and shows xenia effect, because the pollen-grain brought in the dominant gene, and the embryo is homozygous recessive because the male gamete which fertilized the egg came from a plant of the same variety as the female parent. The converse is also possible. The endosperm may be homozygous without xenia and the embryo may be heterozygous and then show xenia effect.

Metaxenia is the term used to describe the effect of foreign pollen on other tissues belonging to the mother plant, outside the endosperm and embryo. This is sometimes noticed in the fruit and seed-coats In cucurbitaceous fruits, the skin colour is affected by the pollen-grain ; in oranges, the colour and flavour of the fruit is influenced by the pollen parent. The same is true of fuzziness and hair length in cotton. It has been suggested that metaxenia effects may be due to certain hormones secreted by the endosperm and embryo. This is based on the observation that the hormone content of the ovary increases after pollination.

CYTOPLASMIC HEREDITY

There is now no doubt that most of the hereditary traits in an organism are determined by genes residing in the chromosomes and that the bulk of heredity is transmitted through the chromosomes. In recent years, some evidence has been accumulated which shows that a small portion of hereditary transmission may take place through the cytoplasm. It is well-known that the egg contains comparatively large amount of cytoplasm, while the male gamete, in most cases, consists primarily of nuclear matter and contains very little or no cytoplasm. Cytoplasmic heredity is, therefore, usually only maternal. It is supposed that self-perpetuating hereditary units are also present in the cytoplasm, apart from the nuclear genes. These have been called **plasmogenes**. All the plasmogenes in an organism taken together represent the totality of cytoplasmic heredity and constitute the **plasmon** whereas one complete set of nuclear genes contained in an haploid set of chromosomes is known as genome. The plasmogenes are distributed in the general cytoplasm and are not arranged in a single file, as the genes are. As there is no mechanism for their segregation comparable to the highly precise mechanism of mitosis for the equational distribution of genes, the distribution of plasmogenes in the daughter cells is not orderly

and regular like that of the chromosomal genes. A cell may contain an indefinite number of them instead of a fixed number.

An outstanding example of cytoplasmic inheritance in plants is provided by the chloroplasts which give to the plants their characteristic green colours. These are self-perpetuating bodies which arise in the cytoplasm from tiny particles called plastid primordia which contain the hereditary material DNA. They are transmitted to the offspring through the cytoplasm of the egg cell. The development of chlorophyll in the plastids, however, is controlled by nuclear genes. Thus, the albino (white) character which appears in some maize seedlings in due to a recessive nuclear gene.

In many cases, however, variations in leaf colour, which occur in variegated leaves are the result of mutations in cytoplasmic genes (DNA) and are not related to nuclear genes In such leaves pale green (or even white) and dark green patches occur in the leaves It is believed that besides the normal plastids, which produce the green colour, there are mutant plastids which produce the pale colour. During cell division a chance distribution of normal and mutant plastids takes place. Some daughter cells receive only or more of normal plastids and develop deep green colour. Others receive only the mutant plastids or more of them and develop white or pale green colour. The result is the mottled appearance of variegated leaves.

According to another hypothesis, colour variation in variegated leaves is not due to segregation of normal and abnormal plastids at the time of cell division but due to the segregation of plasmogenes in the cytoplasm of somatic cells or ovules. These plasmogenes affect the size of the plastids and the development of colour in them. An interesting example is that of the four-o'-clock plant (*Mirabilis jalapa*). Single plants often bear three kinds of branches—green, white and variegated. Seeds borne on green branches produce green plants, those on colourless branches produce albino seedlings while those borne on variegated branches may give rise to albino or green or variegated plants. This inheritance takes place through the ovule cytoplasm and the male gamete has no effect as it contains but little cytoplasm.

Another example of cytoplasmic heredity is a case of male sterility described by Rhoades. The pollen is abortive but the ovules are normal. This trait is transmitted through the ovule parent and never through the pollen parent. Rhoades removed each of the chromosomes of the male sterile race, a different one in each case,

and in its place introduced a similar chomosome from the normal strain. In no case was any change in male sterility affected, showing that the trait was not carried on any chromosome. It seems to be controlled by some factors residing in the cytoplasm, independent of the chromosomes.

An important feature of inheritance of characters controlled by nuclear genes is that reciprocal crosses give identical results. The results are the same whether the mating is A male×B female or B male × A female. The only exception, and for which there is a genetic explanation, is provided by the sex-linked characters. In the case of cytoplasmic inheritance the reciprocal crosses give unlike results. This is necessarily so because cytoplasmic inheritance is mainly maternal and a character will appear in the progeny only if it is present in the maternal parent.

All cases of maternally transmitted characters are not due to cytoplasmic inheritance. As the egg develops in the body of the mother, its cytoplasm is subject to the effect of substances produced in the mother's body and is also influenced by the mother's genes. This affects some of the characters of embryo. This effect of the maternal genes on the egg cytoplasm is called **predetermination** and the characters affected are said to be predetermined. Such effects are passed on through the cytoplasm and are not due to any hereditary units contained in the cytoplasm.

An example of maternal effect of this type is the *direction of coiling* in snails. In some strains of snails the shells have right-handed (dextral) coiling while others show left-handed (sinistral) coiling. This trait is not related to the genotype of the snail but is determined by the effect of the genes in the cells of the mother on spindle formation in metaphase of the first mitotic division of the zygote. In dextral strains the spindle is tilted to the right and in sinistral strains to the left. The genes introduced into the zygote by the sperm or the egg have no effect on this phenotypic character.

Sometimes phenotypic changes are produced as a result of the effect of environmental factors or chemicals and are transmitted through the egg cytoplasm. The changes so produced persist for a few generations, gradually diminish and finally disappear. These are called **dauermodifications**. These are not gene-controlled characters and do not behave as Mendelian traits nor are they determined by any stable hereditary units contained in the cytoplasm. They represent the lingering but transient effect of some

environmental factor on the cytoplasm. Stable hereditary characters due to some specific quality of the cytoplasm must, therefore, be distinguished from cases of predetermination and dauermodification on the one hand, and from gene transmission on the other. Only after these have been eliminated could a character which maintained itself through successive generations be regarded as a case of cytoplasmic inheritance. Moreover, the stableness of the characters should be proved by back-crossing with the parental type.

QUESTIONS

1. In mice the genotype *yy* is grey, *Yy* is yellow, and *YY* is lethal in the embryo stage. What offspring would be expected from a cross between a yellow and grey ? Between two yellows ? In which cross would you expect the largest size of the litter ?
2. In Cocker spaniels, the genotype *A—B—* is black, *aaB—* is silver, *A—bb* is red, and *aabb* is lemon. A black cocker is mated to a lemon one and produces a lemon pup If this black dog is mated to another of his own genotype what proportions would be expected among the offspring ?
3. In chickens, comb shape is conditioned by two pairs of genes. The various genotypes and their associated phenotypes are as follows, where dash indicates that either allele may be present.

   R–pp=Rose comb   *rrP—*=Pea comb
   R—P—=Walnut comb   *rrpp*=Single.

   A pure walnut is crossed to a single. Give the phenotypes and genotypes of the F_1 and F_2. What is the phenotype ratio if the F_1 is back-crossed to the single comb parent What percentage of rose will be expected in the F_2 of the first cross of single comb ?
4. Will the result in the F_1 and F_2 be different if the parents in *Q*. 3 are pure rose comb and pure pea comb ?
5. In chickens the dominant gene *R* gives rose comb, and the dominant gene *P* gives pea comb. When *P* and *R* are present together, the comb form is walnut. The homozygous recessives of *P* and *R* produce single comb. Determine the comb form of the offspring of the following crosses :

   RrPp×*RrPp*   *Rrpp*×*RrPp*
   rrPP×*RrPp*   *Rrpp*×*Rrpp*
   rrPp×*RRPp*   *rrPp*×*Rrpp*
6. A rose crossed with a walnut produces 3 walnut, 3 rose, 1 pea, and 1 single. Give the genotypes of the parents.
7. Walnut×single produces walnut rose, pea and single in equal numbers. What are the genotypes of the parents ?
8. In sweet peas genes *C* and *P* when alone produce white flowers. When both are present the flower colour is purple. Give the flower colour of the offspring of the following crosses :

   CcPP×*CcPp*   *ccPp*×*CcPp*
   Ccpp×*ccPp*   *CCpp*×*ccPP*

9. A purple-flowered plant crossed with a white-flowered plant gives 81 purple and 54 white (5/8ths : 3/8ths). Give the genotypes of the two plants.
10. Purple-flowered × white gives 50 per cent purple and 50 per cent white. Give the genotypes of the parents.
11. In summer squash, the gene for white fruit colour (*W*) is epistatic to that for yellow (*Y*) which is dominant over green (*y*). Determine the fruit colour of the offspring of the following crosses :

    WwYy × *Wwyy* , *wwYY* × *Wwyy* ; *Wwyy* × *wwYy*.
12. White squash plant is crossed with yellow. The progeny consists of 1/2 white, 3/8 yellow and 1/8 green. Give the genotypes of the parents
13. White × Green squash plants produce 1/2 white and 1/2 yellow offspring. Determine the genotypes of the parents
14. White × White squash gives 3/4 white, 3/16 yellow, and 1/16 green offspring. What are the genotypes of the parents ?
15. A green maize plant when selfed produced about 15/16 green and 1/16 white (lethal) seedlings. Find out the genotype of the plant and the mode of inheritance of the pigment.
16. Some character, like panicle length, is often much more variable than another character, like weight of grain. Explain the reason.
17. *Suppose that skin colour in man is influenced by two factor pairs A-a and B-b so that AABB is "black" and aabb "white" and between these are "dark"; "medium" and "light" skin colours A, medium × light negro cross gives 1/8 dark, 3/8 medium, 3/8 light, and 1/8 white. What are the genotypes of the parents ?*
18. Making the same assumption as in the previous question find the genotypes of the parents in the following mating:

    Medium × Light gives 1/2 medium and 1/2 light.
19. What is more probable ? Two negroes begetting a white-skinned child, or two white-skinned people begetting a dark-skinned child ? Explain
20. A light coloured man is married to a white woman. What can be the darkest colour of their child ?
21. What could be the darkest colour of the child if both parents are light ?
22. A black man is married to a dark woman. What could be the lightest colour of their child ?
23. Assume that in tomatoes the genotype *aabbcc* produces 3-ounce fruit and the genotype *AABBCC* produces 6-ounce fruit, each dominant factor adding 1/2 ounce fruit weight Cross a homozygous 3-ounce plant with a 6-ounce one. What will be the phenotypes of the F_1? of the F_2 ?
24. On the basis of the above assumption, determine the range of fruit weight resulting from the following crosses of tomato plants :

    AaBbCC × *aaBbCc* *AaBbCc* × *AabbCc*

    AABbCc × *AaBBcc* *aaBBcc* × *AABBcc*

    AAbbcc × *aaBBcc* *AAbbcc* × *AabbCc*
25. In maize there is a yellow-grained variety and a white-grained variety. Grains from a pure breeding yellow variety (*YY*) and a pure white variety (*yy*) are sown alternately with each other. At maturity the cobs on the white variety contain mixtures of white and yellow grains. How would you account for this ?

8

HEREDITY AND ENVIRONMENT

In the earlier chapters of this book we have described the effect of the various factors of the environment on the structure and functions of plants and it was emphasised that the characters of a plant are greatly influenced by the environment. A change in the environment is often accompanied by perceptible changes in plant. From the study of heredity, we learn that a character of an organism is determined by its genotype. The question naturally arises what is the relation between heredity and environment? What is more important, heredity or environment ? seed or feed ? nature or nurture ?

There are pea plants, for example, some that are tall because they have a gene for tallness, and others that are dwarf because they have only the genes for dwarfness. Does the gene for tallness always produce a tall plant ? If two seeds of almost the same size and weight are selected from a plant which is homozygous for tallness, and are sown, one in well-watered good garden soil and the other in a soil that is poor in minerals and has an inadequate water supply, the plants that are raised from them will be very different. The one that grows in good soil will be tall like the parent and the other will remain stunted and dwarf. Evidently, the two plants possess the same genes for stem length and yet their phenotypes are different. It is a well-known fact that in crop plants, yield and quality are controlled by a number of genetic factors. Yet, the results obtained in actual practice are greatly influenced by several environmental factors. Best results are obtained only when the soil is well-manured and contains an adequate supply of water, and temperature and light are optimum. Breeds of cattle have been

produced which are known for their high milk yield. The character is hereditary and is due to a certain combination of genes. Similarly, the "white leghorn" variety of fowl is famous for the large numbers of eggs that it lays in a year. But the number of pounds of milk or the dozens of eggs produced are greatly affected by the amount and kind of food given to a cow or a laying hen. In each of the above cases, the impact of the environment results in modification of the trait mentioned. Such modifications of phenotypic characters are referred to as environmental variation in contrast to the genotypic variations which are due to different forms (alleles) of genes or different gene combinations.

It is clear from the above instances that the same gene in one set of environmental conditions produces one character and in another set of environmental conditions another character. Genes control characters but they show their effect only if they have the proper environment. But no amount of control of the environment will develop a character in an individual unless the necessary genes are present. All characters, therefore, depend upon the interaction between genes and environment. A character is the visible effect of a gene in a given environment. An organism is the product of the genes and the environment. Change either the gene or the environment and the end result will change.

It is not the characters as such that are inherited. Only the genes are inherited. How a particular gene will express itself will be under the influence of the environment. Consider a green plant. It develops chlorophyll because of the presence of certain specific genes. If this very plant is cut off from light, it will remain pale-yellow. The same condition arises in the absence of iron, magnesium or manganese. What the green plant had inherited was not the green colour but the ability to produce green colour in the presence of light. A favourable environment is necessary for the genotype to develop the characters. What the genotype determines is the mode of reaction of the organism to the environment. This is nicely illustrated in the examples of fowls and Himalayan rabbits described below.

There are breeds of fowls which breed true for yellow legs and others which breed true for white legs. The difference is due to two alleles of a single gene, yellow legs being dominant to white legs. But this holds good only if they are fed on normal diet. If they are fed on white maize, birds of the normally yellow-legged breed will have white legs. To show yellow colour, their genes have to

interact with a chemical substance found in yellow maize (and also in green vegetables), but not in white maize. Likewise, the pea plant which had a gene for tall size remained dwarf due to unsuitable conditions.

The Himalayan rabbit has a white coat which is recessive to the ordinary brown agouti colour of the wild type. The difference is due to a single factor-pair. The factor in the Himalayan rabbit produces white hair at the Mammalian optimum temperature, but black hair at a lower temperature. At birth, all the Himalayan rabbits are uniformly white, for the whole body has been maintained at high and constant temperature before birth. But subsequently the extremities, the ears, the muzzle and feet, which are subject to chilling, turn black, for these parts are cooler than the rest of the body and this difference is sufficient to totally alter the effect of the Himalayan factor. That this explanation of temperature effect is correct has been proved experimentally. If a patch of hair be shaved off the back of two Himalayan rabbits and the one be kept in a warm and the other in a very cold place, the hair which grows again will be white in the former environment and black in the latter.

An instance of the interaction of genetic factors with the environment may be cited from the plant kingdom. In barley, there is an unusual variety of viable albino (white). The character is due to a single recessive factor, but it can only produce the completely albino types when the plants are grown below 2·5°C. Above 18°C they develop the full amount of green colour and cannot be distinguished from the genotypically green plants.

The effect of environment is patent in the case of aquatic plants in which a part of the shoot is immersed in water and a part grows above it. The immersed leaves are often different from the leaves that are above the surface of water (*e.g.*, *Ranunculus aquatilis*) although all the leaves have the same genotype.

In man, also, there are many instances of the interaction between genetic factors and environment. A negro develops the black colour because it has dominant pigment genes. A member of the white race, who lacks the pigment genes, living an outdoor life in the tropics where he is exposed to abundant and intense sunlight, also develops the colour pigment as evidenced by his sun-tanned skin. Only the rate of pigment development in a white man under the influence of sunlight is much slower than in the case of a negro whose genotype causes the pigment to develop rapidly within a few

days after birth and the skin to become dark independently of sun exposure. Here, the genotypic difference is related to the different rates of pigment formation. Many of the genotypic differences in plants and animals are the outcome of differential rates of physiological processes.

Human intelligence and social behaviour are also controlled by genes. Every one inherits from his parents a certain quota of intelligence measured by the so-called *I.Q.* (intelligence quotient). But what one makes of it depends in a very large measure on the education, training and the diet that one receives and social conditions of the environment What is inherited is not a certain degree of intelligence but the capacity to develop a certain degree of intelligence, given the proper conditions. As a result of the impact of such factors of the environment, an individual who starts with a lower *I.Q.* may eventually catch up and overtake an initially better-endowed person. There is a famous Punjabi saying, "The Ak (*Calotropis*) will produce an ak and the mango a mango." This emphasises the role of heredity But you can't get good mangoes without good environment.

An excellent material for studying the relative importance of heredity and environment is provided by human twins. Twins are of two kinds : fraternal and identical. Fraternal twins are developed from two separate eggs, one from each ovary, fertilized by two separate sperms. They are also called, dizygotic twins. They may belong to the same or to different sexes and the degree of resemblance between them is no more than between ordinary brothers and sisters born at different times, for they are entirely independent individuals with different heredities. Identical twins are produced from a single fertilized egg which in its early stage of development is divided into two independent parts, each of which develops into a separate embryo. *Such twins are also described as monozygotic.* As they develop from the same zygote, they have the same heredity and belong to the same sex.

When the identical twins are brought up in the same environment, the resemblance between them is of a remarkable degree. They have the same features, physique, size, facial expression, voice, colour of hair or eye. They belong to the same blood group. Even their mental traits and temperaments are very similar. Their fingerprints also show close resemblance except that they are the mirror image of each other. The resemblance between the twins is, in fact,

so great that quite often it is difficult for even the mother or wife to tell one from the other.

When the identical twins are reared separately in different environments, the resemblance between them is still very close and slight differences between them can be explained on the basis of the differences in their environment. Intelligence tests made by Mullar on a pair of identical twins, reared apart, revealed that one twin scored 153 marks, an exceptionally high-rating, and the other *scored 156. This is a very close resemblance indeed. In* another pair investigated by Newman the *I.Q.* ratings of two identical twins were 123 and 127 This also shows a close correlation. The difference in the intelligence of the two pairs could be readily attributed to their different heredities and the close approximation in each pair could likewise be attributed to their identical heredities. In other studies of twin pairs somewhat larger differences were encountered in the *I.Q.* of two twins of a pair and this could be explained as due to greater difference in their environment, *e.g.*, education, training and social influences. In such cases, also, it was found that the identical twins showed a greater correlation than existed between the fraternal twins.

Occasionally, identical twins are born more or less joined together. They are called **Siamese twins**. They remain in this condition unless surgically separated by skilled hands. In the case of Siamese twins, one may get sick and even die before the other but the second will die within a few hours unless he is separated from his twin.

There is evidence that in the matter of susceptibility to diseases the identical twins show a greater correlation than there is between fraternal twins. The Los Angeles twins, Victor and Eugene, had their appendix removed the same day (36 years). They began getting grey hair at exactly the same time. The corrections for their *eye glasses were identical and the same corresponding teeth had* been pulled and filled.

Thus, heredity and environment both work hand in hand. What is passed on by the parents to the offspring is a certain set of genes. Only the genotype is relatively constant ; the phenotype constantly changes during the life of an organism. You may see this yourself by comparing a series of photographs of a person taken in childhood, early boyhood, mature youth and old age. But, although the phenotype registers the effect of the environment, the genes are highly resistant to the forces of the environment.

A person whose growth was stunted on account of poor diet and unhygienic environment or due to disease will pass on to his children the capacity to develop sound and well-built bodies. Similarly, a person who was well-endowed mentally at his birth but remained backward due to lack of opportunity can still pass on to his children the capacity to develop high intelligence. The hereditary potentialities of an organism are normally not affected by environment.

Each one of us is born with thousands of genes, received from the parents. As the number of combinations of genes, which are possible, is infinite, each one of us is born with a different set of genes of which there is almost no possibility of duplication, except in the case of identical twins who are descended from the same zygote (monozygous) and are necessarily identical in their gene assembly. The entire combination of genes which each one of us inherited from our parents resulted entirely from chance. It thus comes to be that genetically all men are not created equal. All of us do not inherit the same capacities and potentialities. These inequalities are the result of a mechanism of heredity over which even a genius has no control. To this inequality is added the inequality of opportunity as well. As a result, few of us ever develop to the utmost our inherited abilities. Only in an ideal world would it be possible to provide to every individual the best possible environment to enable him to develop his hereditary potential to the maximum. Unfortunately, ours is a world that is far from being perfect and ideal.

Does environment affect all hereditary factors and the traits that they control ? The answer is in the negative. Different traits differ markedly in their susceptibility to the influence of the environment. In man, for example, the blood group, colour of the hair and eye and many other physical traits are determined absolutely by heredity, and environment has no influence on them. The effect of environment on hereditary traits is, therefore, not a universal one. The relation of these forces has to be considered separately for different traits.

QUESTIONS

1. Is flower colour present in the oospore ? Is it correct to say that colour itself is inherited ? What in this connection is inherited?
2. Which is more correct to say : that traits such as height of plant and fruit colour are inherited or that they develop. Name the two factors necessary for the development of traits in general.

9

HYBRID VIGOUR

IT has long been known that in naturally cross-fertilising species inbreeding leads to marked deterioration in the progeny. The general result was loss of vigour, and reduced fertility and productivity. Many lethal and subvital types, for example, albinos, chlorophyll deficiencies, dwarfs and other defectives, appeared. The loss in vigour through successive generations was so pronounced that many forms could not survive even under the most favourable conditions. This inbreeding depression was noticed by early experimenters both in plant and animal species.

The deleterious effect of selfing was proved experimentally, independently by the work of East and Shull on maize. It was observed that after a few generations of selfing the crop yield fell to one-half, and in some cases to one-third of that of the open pollinated variety and several types turned out to be so weak that they were scarcely able to maintain themselves. The deterioration was more marked and rapid in alfalfa, a cross-pollinating legume. Only a few lines could be maintained beyond the third selfed generation. Similar drastic results of inbreeding were observed in carrots.

The depressing effects of inbreeding are, however, not universal. In many plants, like onion, rye and sunflower, the harmful effect of inbreeding was found to be quite small. Sometimes, matings between closely related individuals of a species was considered desirable. Such human marriages were favoured in many countries in the past for the sake of preserving the "superiority of blood." The marriage of Cleopatra, queen of Egypt, with her half-brother Ptolemy is a well known historical example of this. In England, even now members of the royal family are normally not permitted to marry a commoner. In live-stock breeding it has been a common

practice to mate outstanding bulls to their daughters and grand daughters. The inbred stock sooner or later showed decline in vigour and fecundity and outcrossing became necessary. The system now consists of inbreeding to concentrate desirable qualities combined with outbreeding to prevent degeneration followed by more inbreeding.

Among plants also there are many species in which inbreeding does not lead to any depression. Self-pollinating species obviously belong to this category, but this is also true of many cross-pollinating species. In this category fall cucurbits and hemp, the former monoecious and the latter dioecious.

As in the case of live-stock, so in plants also that suffer from inbreeding depression, vigour and fertility can be restored by again crossing the inbred lines. The hybrid offspring of such matings are taller, sturdier and more productive than the better parent. This superiority of the hybrid is known as **hybrid vigour** or **heterosis**.

Hybrid vigour is a very common phenomenon and is observed in all offspring resulting from outbreeding. Even species that seem to suffer little or not at all from inbreeding frequently benefit from crossing.

Hybrid vigour occurs both in plants and animals. It may manifest itself not only as greater height and weight, but also in many other forms, such as increased yield of fruit, larger seed and more efficient seed germination, more luxuriant vegetative growth in tobacco and forage crops, greater resistance to disease, tolerance to drought or cold, earlier flowering, longevity, increased milk production in cattle, more egg-laying in poultry, greater silk production by the silkworm, and various other manifestations of better fitness. Hybrid vigour is not a newly-discovered phenomenon. The mule, hybrid between jack and a mare, was used by ancient man for its well-known qualities of strength and stubbornness. Kolreuter and other early hybridisers were aware of it. Darwin had also observed from his experiments that inbreeding in plants resulted in a degeneration of vigour and that the offspring produced from crossing different strains showed hybrid vigour.

The best example of heterosis is hybrid maize (corn). The use of hybrid maize varieties in the United States has resulted in an increase of about 15 bushels* per acre giving an aggregated increase of 900 million bushels per year for the country without

*A bushel is a dry measure of 8 gallons for measuring grain, approximately 60 lbs.

any increase in land and labour. Greater heterosis was observed among hybrids of parents of differing origins than among hybrids of closely related parents. In addition to yield, other desirable qualities, such as a strong root system, uniformity in the size of ears, and resistance to drought, disease and storm damage are often combined in one strain. In America, almost the entire corn growing land is sown with hybrid seed. In India, high yielding hybrid maize varieties Ganga 101, Ganga 3, Ganga 5, EH 238, EH 461 and EH 450 for the plains and VL 54 and Him 123 for the hills have been produced.

An important point to remember is that hybrid vigour is an unfixable trait. It decreases rapidly in the second (F_2) generation, and diminishes in each succeeding generation. The grower of hybrid maize is, therefore, warned against saving seed from the resulting crop for future sowing. In order to obtain high yield, fresh hybrid maize seed must be obtained each season.

GENETIC EXPLANATION OF HETEROSIS

Although hybrid vigour is a familiar phenomenon and its effects are sometimes spectacular, its causes are not completely understood. According to one hypothesis, heterosis is due to many pairs of genes for strength, vigour, fertility, etc. One strain has some of these genes in dominant form but lacks others, whereas in the second strain the condition is just reversed. Crossing of the two brings all the dominant favourable genes together in the hybrid in which the harmful effects of the recessive genes contributed by one parent are suppressed by their dominant alleles brought in by the other parent. Hence the heterozygote is taller, sturdier, more vigorous and more productive than either parent. When the hybrids are inbred, segregation and recombination will occur and will produce homozygous recessives, in which the harmful recessives will no longer be masked by their dominant alleles. The result is a diminution of vigour.

There is an important flaw in the above explanation. According to this hypothesis, inbreeding of the F_1 hybrids should also produce in the F_2 generation some offspring which would be homozygous for all the dominants. Such offspring would always breed true for hybrid vigour. But, as stated above, one of the peculiarities of hybrid vigour is that it is unfixable. There is a progressive diminution of hybrid vigour in the F_2 and succeeding generations and all experiments to recover and to

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preserve homozygous dominants for vigour have failed. On the basis of the above hypothesis it ought to be possible. We, therefore, have to conclude that the explanation is inadequate.

Jones has modified the above explanation to meet this objection. According to him, size and vigour are determined by a large number (perhaps thousands) of genes scattered over several or all the chromosomes. The effect of these genes is cumulative. On each chromosome are some favourable (dominant) and some unfavourable (recessive) genes, linked together. No inbred parent, therefore, has all the genes favourable to development. Two dissimilar parents differ in the assortment of favourable and unfavourable genes. The F_1 offspring of a cross between two dissimiliar parents will have the dominant members of each pair. This unique combination of favourable genes will bring about a unique masking of their unfavourable alleles. All the F_1 hybrids have the same genetic constitution and would show the same degree of hybrid vigour. When the F_1 hybrids reproduce among themselves, and if there is no crossover, only a few of the F_2 offspring will have the optimum combination of favourable genes. Most of the F_2 offspring will have one to many unfavourable recessive genes in the homozygous (and therefore unmasked) condition. Therefore, the average amount of vigour will be much less than in the first generation.

The multiple factor hypothesis of Jones may be illustrated by an example. Suppose height is determined by 8 pairs of alleles (*Aa, Bb, Cc,......Hh*) distributed on four chromosomes, and suppose there are no crossovers between the chromosomes. The two parents will have the genotypes as under :

PARENT 1	PARENT 2
AA bb CC dd EE ff GG hh	*aa BB cc DD ee FF gg HH*

and their gametes will be

A b C d E f G h	*a B c D e F g H*

If the dominant genes (in the homozygous and heterozygous condition) provide 3 units each towards height and the recessive genes (in the absence of dominants) provide 1 unit, and if the effects of different genes are additive then the height of both parents will be 16 units. The F_1 hybrid, formed by the union of their gametes, will have the gene composition :

A a b B C c d D E e f F G g h H

and its height will be 24 units, and it will show considerable vigour.

According to another hypothesis put forward by East, hybrid vigour is due to the heterozygous condition itself, which provides some physiological stimulus to growth and development. Somehow, the effect of gene *A* is intensified by the presence of its allele *a* on the homologous chromosome, but not by another *A*, so that the gene combination *Aa* has a greater effect than *AA* or *aa* have. Maybe that the two alleles affect two different but related aspects of the same process. This concept is known as overdominance hypothesis of heterosis.

HYBRID VIGOUR IN OTHER ORGANISMS

Hybrid vigour has been utilised in the improvement of tomato, tobacco, squash, cucumber, egg plant, cotton, sugar beet, onion, forage crops and cereals like maize, millet, sorghum and other useful plants. It has also been demonstrated in many ornamental flowering plants and in the fungus *Penicilium* in the production of penicillin. It has also been exploited in animals. Hybrid hen lays many more eggs in a year than the average standard strains ; and crosses between the Yebu and English type cattle have been produced to suit the hard climate of North Australia. Crosses between the Red Sindhi breed of Indian cattle and the Jessey breed of America give 30% more butter fat per cow and are heat resistant. Pork yield in pigs and silk production in silk worms have similarly been greatly increased. A careful exploitation of hybrid vigour in cultivated plants and domestic animals can bring about a great increase in the world's production of food and clothing, and can contribute towards the solution of many a problem of man.

Crossing of dissimilar plants does not always lead to heterosis. To this category belong plants like wheat and barley which are mostly self-pollinated in nature. Inbreeding in these plants also does not result in degeneration of vigour. The explanation for this is as follows. Self-fertilization sorts out the recessive genes and in a few generations produces forms which are pure breeding recessives. The deleterious recessive forms are weak and are quickly eliminated by natural selection because they must stand or fall on their own merit. Only favourable genes survive and they are also in homozygous forms (*AA BB CC* ..etc.) that have adapted themselves successfully to the environment in the course of evolution. Self-pollination of these successful strains only perpetuates their homo-

zygosity and leads to no loss of vigour and outbreeding causes no heterosis.

The majority of our valuable fruit trees, vegetables and garden plants are the result of so many cross-pollinations that they are heterozygous for most of their desirable genes and possess hybrid vigour to a marked degree. On account of the very fact that they are hybrids they seldom come true by seed because of segregation and recombination and resulting homozygosity for many genes which causes loss of hybrid vigour and the appearance of undesirable traits. That is why many of them are propagated vegetatively. Thus, apples and pears are multiplied by grafting, peaches and plums by budding, grapes by cuttings, and strawberries by runners. Each new individual in such cases is really a part of the old plant and has all its qualities, good and bad. All 'Golden Delicious' apples are alike, as if borne on the same tree and all the plants retain the vigour and productiveness of the original hybrid from which they are derived. Ornamental plants like dahlias, chrysanthemums, roses, and the farm plants like white-potatoes, sweet potatoes, and sugar-cane rarely come true by seed because they are hybrid. They are, therefore, propagated vegetatively. Hybridisation produces valuable plants and vegetative propagation preserves their valuable characters and vigour.

QUESTIONS

1. What is heterosis ? How would you account for it ?
2. Give examples of hybrid vigour from the plant and animal kingdoms
3. In self-pollinated crops, hybridisation does not result in hybrid vigour and inbreeding does not cause deterioration. Comment on this statement, giving reasons.

10

MUTATIONS

MUTATION

WE have learnt that hereditary traits are due to the action of genes borne on the chromosomes. Till the first quarter of this century the genes were regarded as stable structures incapable of changing. The heredity of an organism was thus regarded as fixed. Then the work of Muller showed that the genes were capable of undergoing a change and thereby became somewhat different from their original form. Such a change would be accompanied by a change in the effect of the gene on the character that it controls. In other words, a change in the gene would change the heredity of the individual. Such gene changes are known as **mutations**. Besides changes in the gene, hereditary changes are produced in many other ways. In the broader sense the term mutation covers all kinds of hereditary changes, whatever the manner of their origin ; and in the narrower sense it is used for gene changes only. In this book the term is used in its broader sense.

By **mutation** then is meant a change of heredity other than the one due to Mendelian segregation or recombination. This term was first used by De Vries to describe sudden and drastic heritable changes in the population of a species and covered only large perceptible changes that appeared in the genotype of a pure breeding variety and bred true. Such changes had been observed earlier also by many people. Darwin had called them **sports** and Bateson referred to them as **discontinuous variations**. The term, as used these days, includes all kinds of changes in the genotypes whether they are small or large. Large and sudden mutations with large

phenotypic effects are called **macromutations** and small mutations are called **micromutations**. Most of the mutations are of the latter category and are continuous. Indeed, mutations may be so small that they do not produce any visible effect on the appearance of the individual and require special technique for detection. Mutation process is the mainspring of hereditary variability which serves as the raw material for the building up of evolutionary transformations.

Mutations occur spontaneously in nature or they may be artificially induced in experimental material. The changes effected by mutations may be external or internal, or they may effect the structure or functioning of organisms. Mutations may increase the resistance of plants to certain parasitic diseases or else make them more susceptible. They may increase the virulence of parasitic fungi and bacteria. Mutations are thus important not only in evolution but also in plant breeding.

There are three principal kinds of mutations : gene mutations, chromosomal mutations and genomatic mutations or polyploidy.

GENE MUTATIONS

Hereditary characters are due to the effects of genes. The number of genes in a cell runs into thousands. Thus, in *Lilium* the number of genes has been estimated at over 2,000 and in man the estimates place the number between 20,000 and 40,000. These estimates are only modest and the actual number may be much larger. During cell division, each gene synthesises by autocatalysis an exact copy of itself out of the material present in the cell. In this way all genes present on the chromosomes of a nucleus reproduce themselves.

Sometimes, a slight slip occurs in this reproduction and a newly produced gene is not exactly identical with the original that produced it. It is somewhat different. This substantive change in gene reproduction is called **gene mutation**. The mutated gene then reproduces itself just as faithfully as the ancestral gene did until it mutates again.

The effect of a mutated gene may be different from its ancestor on the character or characters that it influences and the only way to discover a mutation is the appearance in the progeny of a pure breeding population of one or more heritable characters not present in the immediate parents. One of the earliest cases of gene mutation that came to notice was in *Drosophila melanogaster*, when in 1909 a single white-eyed individual appeared among the progeny of

a true-breeding strain of red-eyed flies.

A mutation may be dominant or recessive. The former produces a visible change in the trait of an organism which it controls. The recessive mutation would not show up immediately, since it would be masked by an unchanged dominant gene. However, even a recessive mutation may eventually appear in some subsequent generation as a result of segregation and recombination, when it becomes homozygous.

The mutant gene and the original gene are situated at the same fixed point or locus on a particular chromosome and the two are said to be the alleles of each other. It is the only way by which a new allele of a gene can arise. Because a gene is located at a fixed point on the chromosome, a gene mutation is called **point mutation.** It involves a substantive change at some fixed point or locus on the chromosome. A gene may mutate in different directions at various times in the history of the species, giving rise to multiple alleles. Thus, the genes kinkly, curly, wavy and straight for hair form in man are multiple alleles. Sometimes, a gene that has mutated may mutate back to normal. Such **reverse mutations** are, however, not very frequent.

In sexually reproducing organisms, each individual has two genes for a character, having received one from each of the two parents. Out of the two, only one gene mutates at one time ; both do not mutate together. Nor does mutation in a gene affect even the immediate neighbour. This shows that natural mutations are directed by internal factors and not by the environment.

Natural mutations may occur in a gene at any time in development. There is nothing fixed about it. They just happen to come about. While gene mutations are most frequent at the time of gamete formation they may also occur during the division of the zygote or in a vegetative tissue. In the last case they are known as **somatic mutations.** A dominant mutation in a bud will produce a shoot that is different from the others. This is called **bud mutation.** In animals and sexually reproducing plants somatic mutations are of no significance in evolution. They are lost with the individuals. In many plants, the mutant branch, for example, can be used as a starting point for a new race by vegetative propagation. Most of the mutations are recessive, though some dominant mutations are also known. A recessive mutation does not show up immediately because of the unmutated dominant gene. It will show its effe- when, as a result of segregation and recombination, it attain-

homozygous condition. Dominant mutations will show up immediately, but dominant mutations are rare.

Most mutations are small with small effect, often so small that they require special technique and training for detection. Occasionally, large mutations appear. In 1791, a male lamb with short bent legs was born in a Massachusetts farm (U.S.A.). It could not jump over fences. The mutant was used in breeding to establish the famous Ancon breed of sheep. A mutation may be harmful, neutral or beneficial to the organism. Many mutations are lethal and cause the death of the mutant at some stage of development. The large mutations, which produce large differences and which De Vries considered important in evolution, are mostly of this type. Thus, a plant which contains a mutated gene that lacks the ability to develop chlorophyll will die in the seedling stage when the food stored in the seed has exhausted. Most of the mutations are disadvantageous and are ultimately eliminated by natural selection. The reason for this is quite simple. Taking any species of plant or animal, we may be sure that mutations have been occurring in it in its long history. Out of those mutations, the harmful ones have been eliminated and only the useful ones preserved by natural selection. The species is now firmly established because it possesses a combination of advantageous mutations which have adapted it to the coditions of life. Any disturbance in this combination of useful mutations is likely to be of disadvantage to the species just as any slight change that is made at random in a well adjusted complex machine like an automobile is likely to adversely affect its efficient working.

Genes are extremely stable molecules. Mutational changes in them are, therefore, not frequent. It has been estimated by Muller that in *Drosophila*, under natural conditions, the average gene mutates only once in a million generations. Although mutations in any single gene are rare, the aggregate frequency of mutations in the entire gene assembly of a species is not low. This is because the number of genes in each cell runs into thousands, and mutation in one or the other of these thousands of genes will occur every few generations in the life of most organisms. Considering the entire gene complex of a species, it is regarded as well-established that gene mutation is a normal phenomenon in nature.

Different genes vary greatly in their frequency of mutations. This is natural, because each gene has a different molecular structure. All genes are, therefore, not equally stable. Some mutate

more often and more easily than others.

On the basis of causes, mutations are classified into two categories, namely spontaneous and induced mutations. The former are those which arise by themselves under the ordinary conditions in which organisms live and without the application of any external agent by man. The latter are those that are produced in organisms artificially by man as a result of some external forces or agents which are then described as mutagens, The frequencies of spontaneous mutations is quite low. The ultimate causes of mutation in nature are not definitely known but it is known that the frequency of mutations may be greatly accelerated by artificial means. In 1927, Muller announced that the mutation rate in *Drosophila* could be increased several times, sometimes several hundred times the normal rate by exposure to X-rays. Most of those artificially produced mutations were similar to those that occur naturally. Like the natural mutations, most of them were recessives, often harmful or lethal to the organism. In 1928 Stadler had succeeded in inducing mutations in barley by the X-ray treatment. Ultraviolet rays, radiations from radioactive substances and other atomic radiations have been found to be mutagenic.

Muller's discovery at once suggested that cosmic radiation, or some other naturally occurring radiation, may be responsible for spontaneous mutation in nature. Experimental studies have revealed that the amounts of natural radiation are so small that they can only account for less than 1 per cent of the mutations that arise in nature. The problem of the origin of naturally occurring mutations is thus still far from being understood.

Many chemicals have been found to possess mutagenic properties. Among these are nitrous acid, ethyl methane sulphonate (EMS), mustard gas, organic peroxides, alkaloids like morphine, colchicine, caffein and camphor. High temperatures have also been found to increase to two or three times the rate of mutation.

The mutagenic agents described above operate from outside the organism. Some mutagens have been found to reside within the organism and are responsible for automutagenesis. Thus, Ive (1950) found that different strains of the same species of *Drosophila* show different rates of mutation in the same environment. This difference in mutability was related to difference in a single gene, the only effect of which was to increase the rate of mutation in those strains in which it was present. In maize, for example, a gene *Dt* (dotted) causes the gene a_1 to change to A_1 which produces

cyanin pigment in the cells of endosperm and in other parts of the plant. Other genes are, therefore, agents that cause or hasten mutation. Such mutagenic genes favour mutation of many different genes, some more than others while they are themselves stable. Mutagenic agents are also produced in old and decaying seeds and bring about automutagenesis.

Mutation occurs at random, that is, its direction cannot be predicted and is not determined by the requirement of the organism, nor does it occur to fulfil any specific purpose of the organism. It occurs regardless of whether it will be useful to the organism or not. Chance alone determines in which of the number of possible ways a particular gene will actually mutate. This is true of both spontaneous and induced mutations. This statement must be taken with a reserve. There is a limitation to the number of ways in which a gene can mutate. This limitation is determined by the structure of the gene. A gene is a chemical substance. Every chemical substance has its own particular range of chemical reactions. This is also true of the gene which has some fixed physical and chemical properties, which restrict its range of reaction. A gene mutates within that range alone but within that range the nature of mutation is a random process. If it happens to be useful to the organism or the race, it is preserved, otherwise it perishes.

CHROMOSOMAL MUTATIONS

A chromosome is an assemblage of genes arranged in a linear order. The number of genes on any particular chromosome is fixed and the position of each gene on that chromosome is also fixed. For each gene, its neighbours and the relative distance from them are also fixed. Thus, each chromosome is differentiated along its length into qualitatively different segments. In other words, it possesses an architecture of its own. Alterations in this architecture can occur as a result of change in the number of genes or their rearrangement within a chromosome without causing any change in the total number of chromosomes. Such changes have been given the various names of **chromosomal aberrations, chromosomal rearrangements, structural changes in chromosomes,** and **chromosomal mutations.** Chromosomal rearrangement may affect single chromosomes or different chromosomes in the same nucleus and depends upon two kinds of events : transverse breakage of the chromosomes and reunion of the broken ends in a way that is different from the original one. Sometimes,

be expected, because genes influence one another and interact among themselves in the production of traits; the loss of some genes upsets

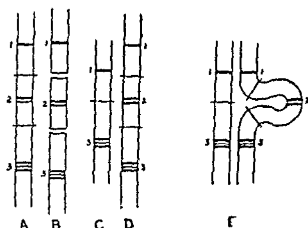


Fig. 10.2. Deletion in the salivary gland chromosome (diagrammatic). A, normal chromosome; B, the middle segment (2) being deleted; C, the reconstituted chromosome after deletion; D, normal homologous chromosome; E, synapsis between the two chromosomes, showing loop formation

the genic balance. When one of the two gametes that unite in syngamy shows deletion of a segment, the zygote formed is said to be a deletion heterozygote. Such a zygote is genetically unbalanced because it will have a single dose of every deleted gene as compared to the double dose of every other gene. An example of the effect of deficiency is the production of the mutant notched wing-margin in *Drosophila*. This is due to the deletion of a segment of the X-chromosome. Deficiencies have also been reported in maize and these result in abnormalities in the phenotypes.

Homozygous deficiencies, that is those that effect both chromosomes of a pair, are usually lethal. This means that almost every gene which the organism has is indispensable, at least in single dose, for the life and development of an organism.

2. Duplication. This is just the opposite of deletion and takes place as a result of unequal cross over during meiosis so that a bloc of intercalary genes is deleted from a segment of a chromosome and becomes attached to its a homologue at any position along its length. When such a cell undergoes reduction division, some of the gametes will carry, at some place on the chromosome, extra genes in addition to the normal haploid complement. This result is called **duplication.** Thus, if a normal chromosome has genes ABCDEFGH, the duplication may be

ABCDEFDEGH or like, as illustrated in Fig. 10.3. Here, the genes *DE* occur twice in the same chromosome of the haploid gamete. The additional genes come from the homologous chromosome which suffers from deletion.

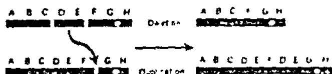


Fig. 10.3 Method of origin of duplication

Sometimes, a block of genes is present more than once in the same chromosome in the form of two successive segments carrying the same genes in the same order. Supposing a chromosome *ABCDEFGH* breaks into three segments like *AB CDE FGH* and its homologue breaks at only one of the two points of this break (in the present instance between *B* and *C* or between *E* and *F*), the internal segment of the first may be inserted in the break of the second in which the sequence of genes after reconstruction will be *ABCDECDEFGH* as shown in Fig. 10.4

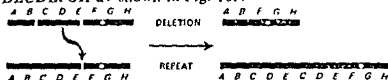


Fig. 10.4. Formation of repeat in a chromosome

This kind of duplication is called repeat because a block of genes has been repeated in the same chromosome adjacent to its original position. Such repeats have presumably arisen in the evolution of the chromosome complement of *Drosophila* and many other organisms by means of duplication.

As a result of duplication, one chromosome of a pair is longer than its homologue and at synapsis will form a buckle, very much as in the case of deficiency. Duplications may be short or long. The additional segment of the chromosome may be repeated two or more times. Small duplications occur in *Drosophila* and are probably of frequent occurrence in nature.

The effects of duplications on development are less deleterious than those of deficiencies, so that relatively long duplications survive. Duplications are of importance both to the individual and the race. Their immediate effect is to produce abnormalities in bodily characters. This is but to be expected, since they alter the genic balance. In a zygote formed by the union of a normal gamete with

With the discovery by Sturtevant and Morgan (1923) of salivary gland chromosomes the 'Bar' (*B*) locus in *Dorsophila* was shown by Bridges to be the duplication of a segment in the *X*-chromosome. The wild female, with only one *B* in each of the two *X*-chromosomes has the normal large eye. Duplications (of the repeat type) in one or both the chromosomes result in smaller size of the eye as shown in figure 10.5. Both 10.5 *C* and 10.5*D* have four bar segments each but the effect on the size of the eye is different in the two cases. The difference depends on the arrangement or position of genes with respect to each other. The phenomenon is an example of the position effect

3. **Inversion.** This is another type of chromosomal rearrangement in which a reversal of a segment of a chromosome takes place. Suppose, a chromosome having a linear arrangement of genes *ABCDEF* breaks into three fragments *AB*, *CD* and *EF*, and the three fragments join again but only after the middle one has rotated through 180 degrees. The order of genes in the reconstituted chromosome will be *ABDCEF*. This is known as **inversion** in a chromosome section. Inversions occur frequently in *Drosophila* as a result of X-ray irradiation and have presumably also occurred in nature as a result of natural radiation.

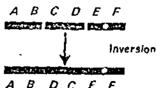


Fig. 10.6. Chromosomal inversion

Sometimes, a part of the inverted segment again undergoes inversion. This is called **included inversion.** Thus, in an inverted

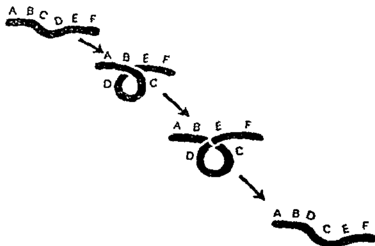


Fig. 10.7. One method by which chromosomal inversion may arise

chromosome *ABEDCFGH* the segment *ED* of the inverted part of the chromosome may undergo further inversion with the result that the reconstituted chromosome will now be *ABDECFGH*.

4. Translocation. Sometimes, a segment of one chromosome breaks and is transferred to another non-homologous chromosome in a cell or to another position in the same chromosome. This is called **simple translocation** Translocations are usually reciprocal and result in interchange of segments between two non-homologous chromosomes. For example, if two chromosomes *ABCDEF* and *KLMNOP* break into fragments *ABC*, *DEF*, *KLM* and *NOP* and these fragments rejoin giving rise to new combinations *ABCNOP* and *KLMDEF*, the case is that of **reciprocal translocation** or **segmental interchange** as shown in figure 10.8.

Reciprocal translocation is like crossing-over except that it involves two non-homologous chromosomes and is sometimes called "illegitimate" crossing-over. Translocations are responsible for varietal differences in many plant species and play an important role in species differentiation. They occur naturally and can also be induced experimentally by X-rays. They have been reported in a

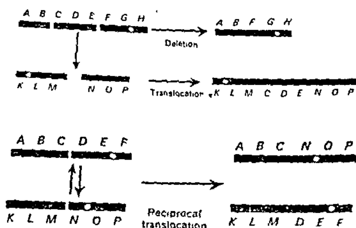


Fig. 10 8. Translocations

number of plant species among which are the weed *Datura stramonium*, *Oenothera*, rice and pearl millet. The term translocation is also used to cover cases in which non-homologous parts of the the same chromosome pair are exchanged.

In translocations no loss or addition of chromosome segments takes place in but the chromosome segments become rearranged and new linkage groups are created. They interfere with chromo-

some pairing in meiosis and thereby reduce crossing over. Imperfect pairing in synapsis causes partial sterility in pollen or ovule in plants with heterozygous translocations, because when meiosis occurs some haploid cells will have deficient chromosomes while others will carry duplications.

Translocations and inversions involve no loss or gain in the genes; they bring about only re-arrangement in the order of genes and a change in the position of some genes and their neighbours. It might be expected that such changes would not cause any phenotypic change in the organism as the gene dose remains the same and no genic mutation, as defined in the preceding section of this chapter, has occurred. Yet, there are instances in which the effect of such chromosomal rearrangement is equivalent to that of gene mutation. In *Drosophila*, for example, in a normal chromosome, the gene hairy is recessive to the normal allele but after translocation, the hairy gene becomes dominant. No gene mutation, that is, change in the nature of the gene, is involved in this case. The change from recessive to dominant in this gene is a simple consequence of change in the position of the gene or of its neighbourhood. Because the rearrangement of the genes in a chromosome seems to have a mutant effect independent of the genes, such chromosomal mutations are called **systemic mutations** or **position effects**. Curly wings in *Drosophila* are the result of inversions. The bar eye gene described earlier is another example of position effect dependent upon repeat. The new arrangement of genes also changes the interaction of the genes with the environment.

POLYPLOIDY

Chromosomes occur in sets and the number of chromosomes in a set is constant for all organisms of a species. For example, in pea a set consists of 7 chromosomes and in maize of 10 chromosomes. The number of chromosomes, which make up the basic set for any species, is known as the **haploid** (N) number. The total complement of genes borne on the haploid set of chromosomes is called the genome. Every reproductive cell or gamete carries this haploid number. When two gametes unite, the zygote and later the individual that develops from this union contains two sets of chromosomes or the **diploid** ($2N$) number. Such individuals have two genomes. When an organism contains more than the usual

two sets of chromosomes, it is said to be **polyploid** and the phenomenon is known as **polyploidy.** Polyploids possess more than two genomes. Polyploidy is, therefore, a genomatic mutation involving increases in the dose of whole genomes. Polyploid plants may have three, four, or more sets of chromosomes and are called **triploids** (*3N*), **tetraploids** (*4N*), **pentaploids** (*5N*), **hexaploids** (*6N*), **hectaploids** (*7N*), **octaploids** (*8N*), **nonaploids** (*9N*), **decaploids** (*10N*), and so on.

In many plants, varieties are known where chromosomes run in multiples af some basic number. For example, there are varieties of wheat with 14, 28 and 42 chromosomes. Seven chromosomes appears to be the basic haploid number in wheats. Wheat varieties with 14 chromosomes are diploid, those with 28, tetraploids and those with 42, hexaploids. Similarly there are varieties of chrysanthemum with 9, 18, 27, 36 and 45 pairs of chromosomes, the basic haploid number in them being evidently 9. Other well-known polyploid series are *Sorghum* species with 10, 20 and 30 chromosomes ; *Oryza* species (rice) with 24 and 48 chromosomes (basic No. 12) ; *Pennisetum* species with 14, 28, 27, 36, 45, 54 (basic Nos. 7 and 9) and *Nicotiana* species with 24, 48 and 72 chromosomes (basic No. 12).

Polyploidy is widespread among plants. In fact, it is more common than the normal diploid condition. Many of our cultivated plants which behave as diploids are really polyploids. The most common type of polyploidy is tetraploidy. The occurrence of polyploid plants would suggest that such forms have been derived from diploids. There is plenty of evidence to show that this is correct. On the basis of the source of the chromosomes, two fundamental types of polyploidy are recognised : **autopolyploidy**, in which the chromosome sets are all of the same kind, derived from the same species ; and **allopolyploidy** in which they are of different kinds, derived from two or more distinct species by hybridisation (Fig. 10.9). In autopolyploids the same genome is multiplied and no addition of any new genes takes place. Allopolyploidy, on the other hand, involves the addition of new genomes. In either case, the polyploid condition arises from abnormalities at the time of cell division. The chromosomes divide normally but somehow normal spindle formation does not occur. The separation of the chromosomes does not take place and cell division fails. All the chromosomes remain in the same reconstituted cell which will now have the double number of chromosomes as compared to the normal cell. Chromosome

doubling is of quite common occurrence in the division of the spore mother cells when, due to the failure of normal meiosis, diploid

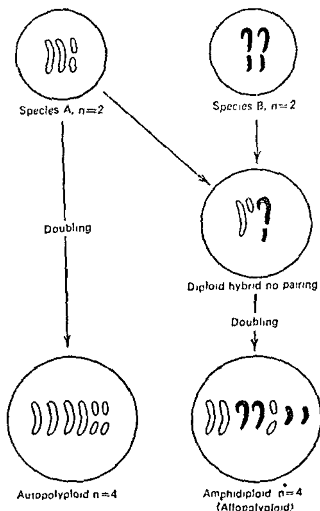


Fig. 10.9. Diagram illustrating the development of autopolyploid and allopolyploid condition. In the latter, the chromosomes of the F_1 hybrid are unlike and do not pair. Doubling of the chromosomes makes pairing possible

gametes are produced. The chance fusion of two such gametes produces a tetraploid plant. Chromosome doubling may occur in the normal diploid zygote or in body cells such as those of the vegetative bud. If this event occurs in a vegetative cell of the growing point or a bud, the cell will be tetraploid. If all the cells in a bud are tetraploid, a tetraploid shoot will develop. This shoot can be used as a starting point for polyploid plants by means of vegetative

reproduction. Sometimes, injury followed by callus formation results in the formation of polyploid tissues. Cell division in callus tissue is irregular and quite often cell walls do not form after nuclear divisions Buds formed from such tissues develop into polyploid shoots. Doubling of the chromosomes can be repeated, leading from tetraploid to octaploid ($8N$) and higher forms.

If the tetraploid plants are fertile and normal meiosis occurs, the spores and gametes formed will be diploid ($2N$). Fertilization between such a gamete and a haploid ($1N$) gamete from the normal diploid plant will result in a triploid ($3N$) form. Triploids may also arise from diploid plants when an unreduced egg ($2N$) is fertilised by a normal gamete ($1N$) or a haploid egg may be fertilized twice by haploid sperms (dispermy). Triploids, pentaploids and others with odd numbers of chromosome sets are completely sterile because normal synapsis between odd number of chromosomes at meiosis is not possible. These plants can be multiplied only by asexual methods as in chrysanthemums, dahlias, roses. Some of the commercially important varieties of apples, pears, bananas, grapes, oranges, guava and pineapple are triploids and are propagated vegetatively.

The study of polyploidy has received a great impetus in recent years by the development of the colchicine method for the production of artificial polyploids. Colchicine is an alkaloid derived from the roots and corm of the autumn crocus, *Colchicum autumnale*, a member of the liliaceae family. In India it is obtained from *C. leuteum*. This drug is a mitotic poison and interferes with the formation of the spindle which is either imperfectly or not at all formed. It has no influence on the doubling of the chromosomes, which proceeds normally. As a result, the chromosomes, which have already been doubled, all remain in a single nucleus giving rise to a tetraploid condition. Colchicine may be applied in many ways. It may be applied as aqueous solution or as solution in agar in liquid form or as a paste in lanoline or gum tragacanth. The paste is applied to the growing buds or cut stems. The solution in water or agar may be dripped on a growing bud or a developing flower by means of a capillary string or dropped at regular intervals. Twigs may be immersed in an aqueous solution and then washed with distilled water or the solution may be sprayed on the growing regions at intervals. Absorbant cotton soaked in the solution may be placed on the growing regions and buds or cut stems. The best method to use colchicine is to soak seeds in an aqueous solution of colchicine after first soaking them in water for

24 hours. When germinated seeds are thus treated, the radicle should be protected as colchicine causes hypertrophy and arrests growth. The concentration required and the duration of treatment vary with different plants and have to be determined by experiment for each species or variety. Ordinarily, a concentration of 0·4 per cent is adequate. Sometimes, much lower concentrations, even up to 0·05%, are effective. Seeds and seedlings treated with colchicine develop into tetraploid plants. Of all the methods, previously used for inducing polyploidy, colchicine treatment is the most effective, yielding 50 to 100 per cent tetraploid plants. A chemical 'Granosan' developed in Russia is said to be as effective as colchicine.

I. **Autopolyploidy**. Plant autopolyploidy is common in nature and in experimental material. Many of our crop and garden plants are natural autopolyploids, for example, millets, maize, rice, gram, lab-lab, cotton, guava, garden nasturtium, chrysanthemum, etc. Muntzing prepared a list of 58 natural autotetraploid plants. One of De Vries' mutants of *Oenothera*, *O. gigas* was an autotetraploid (*4N=28*). In general, these polyploids show a more vigorous and sturdy growth, have thicker and stouter stems, larger and more showy flowers and larger fruits and seeds and often have broader, thicker and darker leaves. Such *gigas* characters of the tetraploids often increase their commercial value. Hairs on the vegetative parts are coarser and thicker. The cells are much larger. The stomata, guard cells and pollen-grains all show an enormous increase in size. In general, the polyploids exhibit gigas character.

Osmotic concentration of polyploids is also higher than that of the diploid plants. Vitamin and alkaloid content, and sugar content in beet are also markedly increased. Plants which are annuals in the diploid state often become perennial when tetraploid or else the season of blooming and fruiting may change. It appears that many of our perennial plants originated from annual plants through polyploidy. The tetraploids are usually more aggressive invaders of new territories and are adapted to more severe conditions of the environment, such as drought and cold. They have, therefore, a wider range of geographical distribution. Polyploidy thus provides a method by which a type may become adapted to new and especially to less favourable conditions. In spite of these facts, the morphological differences between autopolyploids and diploids are only slight. Autopolyploidy, therefore, does not produce new species, but only new varieties or races and consequently is not of much significance in evolution.

The polyploids are reproductively isolated from the diploids. Thus, the tetraploids on being crossed with diploids produce only sterile triploids, whose meiosis is irregular. In meiotic prophase, the autotetraploids sometimes form quadrivalents instead of the normal bivalents. Different chromosomes may then pair at different points along their length. This often results in irregular segregation leading to inviability or partial sterility.

2. **Allopolyploidy.** This is more common than autopolyploidy and most of the natural polyploids are of this type. The most common method of origin of allotetraploidy is hybridisation between two species followed by chromosome doubling. F_1 hybrid is a *diploid* organism containing a set of chromosomes from each of the two parents Such a hybrid is normally sterile. The cause of this sterility lies in the imperfect homology or lack of it between the chromosomes of the two parents. The chromosomes of the two kinds fail to recognise each other in meiosis with the result that synapsis does not occur and gametes are not formed. Thus, an F_1 hybrid between a species with the diploid chromosome complement *AA* and a *BB* species would be *AB*. The chromosomes of the *A* and *B* types being unlike, they do not mate with each other in synapsis with the result that meiosis does not proceed and the hybrid fails to form spores and gametes and remains sterile. This difficulty can be overcome if doubling of the chromosomes takes place. This may occur in the F_1 zygote which will now have the chromosome constitution *AABB*. There will now be two chromosomes of each type in the F_1 hybrid that develops from the zygote. All chromosomes of the hybrid would pair and meiotic divisions will proceed perfectly; normally, resulting in gametes of *AB* constitution. The plants will, therefore, be completely fertile. Doubling of the chromosomes may take place in the diploid (*AB*) F_1 hybrid at the time of spore formation. In some of the spore mother cells, meiosis proceeds but normal reduction divisions fail to occur so that the resulting gametes will have the chromosome constitution *AB*. In a self-fertilised plant, fertilization of some *AB* ovules by *AB* pollen-grains would take place, thus producing the allotetraploid *AABB* at once. Such plants would be fertile. Thus, allopolyploidy restores fertility to inter-specific hybrids which would otherwise remain sterile. The allopolyploid hybrid combines some of the characters of the two parents and also possesses some distinctive qualitative characters which differentiate it from either parent. It breeds true and does not cross with the parental species. It is, thus, a new species formed suddenly.

An important allopolyploid series is that of wheat. Wheats are of three kinds ; Einkorn group with 14 chromosomes ($N=7$; *AA*), Emmer group with 28 chromosomes ($N=14$; *AABB*, *AAGG*), and vulgare group with 42 chromosomes ($N=21$; *AABBDD*). The seriation, 14, 28 and 42, at once suggests that the three types constitute a polyploid series with diploid, tetraploid and haxaploid numbers. The commercial American cottons are also allotetraploids ($4N=52$). The cultivated species of *Gossypium* in Asia and Africa are diploid plants ($2N=26$) and so are some American wild species of *Gossypium*. It is supposed that the cultivated American cotton arose as a result of natural crossing between some old-world species and American wild species of cotton and the doubling of the chromosome number in the resulting hybrid.

HETEROPLOIDY

In polyploids all the chromosomes are present in the cells more than two times. Sometimes, individuals are produced with one or more chromosomes present in triplicate and others lacking in one or more chromosomes. The general condition in which extra chromosomes are present or some chromosomes are missing is known as **heteroploidy** or **aneuploidy**. Such a condition may be derived from a diploid set by the addition of individual chromosomes or from a polyploid set by their elimination. The former condition arises out of the occasional failure of a pair of chromosomes to separate during reduction division. The condition, known as **non-disjunction**, produces abnormal gametes, some carrying an extra chromosome ($N+1$), and some lacking one chromosome ($N-1$). Union of an $N+1$ gamete with a normal gamete (N) in fertilization produces a $2N+1$ zygote. One of the chromosomes will be present in triplicate. Such an organism is said to be **trisomic** for the particular chromosome of which there are 3. Some of the pollen grains formed by the trisomic will carry an extra chromosome. Such pollen-grains are usually inviable so that the trisomic condition is transmitted only through the egg cell. Gametes lacking in one chromosome ($N-1$) are usually inviable, but sometimes their union with normal gametes (N) produces zygotes lacking one chromosome ($2N-1$). These are called **monosomics** ; they have one of the chromosomes present only once instead of the normal two times. Monosomics are usually inviable. Occasionally, individuals are produced which have two extra chromosomes of the same type ($2N+2$). These are called **tetrasomics**. Indivi-

duals which contain two different chromosomes in triplicate instead of two times ($2N+1+1$) are called **double trisomics,** and those in which each of the two chromosomes are present four times are called **double tetrasomics** ($2N+2+2$). Sometimes, plants are produced in which certain chromosomes are wholly absent. These are called **nullisomics.** These are usually sterile. In rice ($N=12$) a nullisomic with $2N=22$ was produced. This was completely sterile and formed no panicles. In wheat (*Triticum vulgare*), $2N=42$), two nullisomics have been isolated. In one of these the chromosome pair number 2 was absent and in the other, chromosome pair XX. Both of these were fertile showing that for normal life and fertility the presence of one of these chromosome pairs is quite enough. In other words, these two chromosomes compensate each other. Polyploids arising from heteroploids are called **secondary polyploids.**

Trisomics have been studied especially in *Datura.* It has 12 pairs of chromosomes, which means 12 kinds, and the extra chromosome may be any of the 12. Accordingly, 12 different kinds of trisomics have been produced, each containing a different chromosome in triplicate. The extra chromosome carries an extra dose of genes contained in the duplicated chromosome. This produces a condition of genic imbalance and, as a result, the trisomics differ from the normal diploid form in the character of the seed capsule and other traits carried by the extra chromosome. The nature of the character differences depends upon the particular chromosome which is present in triplicate, so that it is possible for an expert to tell which chromosome is added.

In *Nicotiana tabacum* ($N=24$), 24 **monosomics** have been produced corresponding to 24 different chromosomes. Each monosomic differs from the other in a specific recognisable character. All of them are weaker than the normal diploid.

The trisomic mutants show greater differences from normal than do ordinary gene-mutants. This condition is much commoner in plants than in animals. It appears that heteroploidy has arisen out of general polyploidy by the loss of certain chromosomes rather than by nondisjunction in diploid forms. Indeed, trisomy arising out of polyploidy may offer a better chance of evolution than does an origin out of nondisjunction. Ordinarily, trisomics are unbalanced and for that reason not likely to become established. But in the evolution of some plants, the condition has become stabilised. This is always in polyploid-derived forms, because

in them the genic imbalance will not be so considerable. The chances of stability increase if, instead of just one chromosome, there are two extras of the same kind ($2N+2$). The two extras could pair at meiosis and remove the difficulty in reduction division which would arise from the presence of an odd chromosome. Getting a pair of extras should be more readily done out of polyploids than out of simple nondisjunction. In self-fertilizing polyploid plants, both egg and sperm of the same individual may have the extra chromosome. Their chance union in fertilization could give rise to a type with two extra homologous chromosomes.

An example of an heteroploid derived from polyploid is that of *Dahlia merckii*. All species of *Dahlia* except this one have $N=8$ or some multiple of 8 ; *D merckii* has 36 chromosomes ($4N+4$). This species is mainly a tetraploid form, in which 6 of the chromosomes are present four times and 2 are present six times (hexaploid=$4N+2+2$). Many of our apples and pears are of similar constitution. Here the basic chromosome number (N) is 7. The chromosome number in these fruit plants is 34 ($4N+6$). This is tetraploid condition in which 3 of the chromosomes are present six times ($4N+2+2+2$), instead of four times. It is believed that heteroploidy in these cases has resulted from the loss of four pairs of chromosomes in hexaploid forms, rather than by the addition of chromosomes.

QUESTIONS

1. How is it that most of the mutations are harmful rather than useful to the organism in which they occur ?
2. Which types of mutations are more frequent ? dominant or recessive ? Which of these are easier to study ? Is there any difference in the way in which gametic mutations of these two types express themselves phenotypically in the offspring ?
3. A blue-eyed man has a brown patch in one eye. How do you account for it ?
4. A man has one eye brown and the other blue. What possible explanations can you give for this situation ? What will be the breeding behaviour of this man ?
5. In the plot of my neighbour is a tree which bears white flowers on some branches and pink flowers on other branches. Give an explanation for it.
6. How can mutations be induced artificially ? What are mutagenic agents ?

7. In barley, usually several tillers (separate stems) arise from the ground, each originating from a separate cell in the seed. In a plant that grew from a X-rayed but otherwise normal seed one of the tillers on self-fertilization produced offspring in the ratio of 3 normals : 1 white seedlings. The remaining tillers produced normal seedlings. Explain these results, giving the genotype of (*a*) the *fertilized* egg, (*b*) the normal tillers, (*c*) tiller which gives the 3 : 1 ratio.
8. Write short notes on the following, giving examples. Simple translocation ; Reciprocal translocation ; Deletion and deficiency ; Duplication ; Repeats ; Inversion.
9. What is polyploidy ? Describe the two principal types, giving examples.
10. Write an essay on gene mutations.

11

NATURE OF THE GENETIC MATERIAL

DNA AS THE GENETIC MATERIAL

We have learnt a good deal about the genes from their behaviour. Essentially, genes are the units of heredity, and in all our discussion so far we have regarded them as particulate material structures that are arranged in a linear row in the chromosomes. They are capable of self-reproduction, a property called replication. In short, the gene is the fundamental biological unit, as the atom is the fundamental physical unit.

Like all material things a gene possesses physical and chemical properties. During the last thirty years, the work of biochemists has given us an insight into the chemical structure of the gene and how the genes control the hereditary traits. The mechanism by which the genes transmit the hereditary characters from one generation to the other is also now fairly well understood.

Chemically, the chromosomes are made of a class of compounds called nucleoproteins. These are formed by a combination of basic proteins and nucleic acids. The common basic proteins are histones and protamines. The nucleic acids belong to two general classes : one containing the sugar deoxyribose and called deoxyribonucleic acid (DNA, for short) and the other containing the sugar ribose and called ribonucleic acid (RNA, for short).

It is now firmly established that in most organisms genes are made of DNA. In other words DNA is the hereditary material. RNA performs an important role in the genetic control exercised

by DNA. The first step which ultimately led to the establishment of DNA as the genetic material was an experiment by Griffith in 1920 on the transformation of Pneumococcus bacterium (*Diplocococcus pneumoniae*). This bacterium occurs in two forms : one, smooth and surrounded by a polysaccharide capsule and causing a severe illness in animals and the second, which is rough and has no capsule and is non-virulent. Griffith injected one group of mice with non-virulent cells and another group of mice with heat-killed virulent cells. In neither case was any adverse effect produced on the mice. A third group of mice was injected with a mixture of non-virulent cells and heat-killed virulent cells The mice developed severe pneumonia and died. The obvious conclusion is that something in the dead virulent bacteria had transformed the non-virulent cells into virulent cells. These transformed cells on multiplication produced virulent cells. In other words, the heredity of the non-virulent cells had been changed by something contained in the dead virulent cells.

In recent years such transformations have been reported in many other bacterial species. In many such cases the transformation was related to the ability to make a certain enzymic protein which catalysed an identifiable chemical reaction within the cell.

Certain bacteria are resistant to penicillin while other closely related forms are susceptible to this drug. When the cells of penicillin-resistant are disrupted and killed, and the debris of these cells introduced into penicillin-susceptible cells, the latter developed resistance to penicillin and transmitted this trait to their daughter cells. Obviously the donor cells had transferred to the recipient cells something which transformed their heredity. The transforming agent in such cases was identified by Avery and his colleagues in 1944 to be DNA as illustrated in figure 11.1. This phenomenon in which the heredity of a cell is changed by introducing pure DNA is called **transformation**. The result is equivalent to the introduction of a new gene. A similar phenomenon occurs when a bacteriophage (bacterial virus) invades a bacterial cell and acts as a natural carrier of the gene. This is called ***transduction***.

DNA is of universal occurrence in almost all plants and animals The only exception is provided by certain viruses in which the genetic material has been found to be RNA. DNA, however, performs this function in the majority of organisms. It is a constant component of all chromosomes and is the chemical of which genes are made. The following observations and arguments support this contention.

all the diploid nuclei of an individual possess approximatly the same amount of DNA.

4. When cells with recognisable chromosomes are treated with Feulgen stain, the staining for DNA is confined almost entirely to chromosomes which have been proved by genetic studies to be the carriers of genes.

5. The quantity of DNA in a given cell is directly related to the number of chromosome sets. Thus the amount of DNA in haploid gametes is almost exactly half that contained in diploid somatic cells of the same species. The first meiotic division of the nucleus which results in the formation of haploid daughter cells brings about an equal division of the DNA of the parental cell between the two daughter nuclei. Syngamy which restores the diploid chromosome condition also restores the DNA content characteristic of the diploid cell.

6. Cells which contain more than the normal two chromosome sets (polyploids) contain proportionately greater amounts of DNA. Thus the DNA content of tetraploid ($4N$) cells is roughly twice that of diploid cells and octaploid ($8N$) cells contain almost four times the DNA present in diploid cells.

7. It is known that the structure of DNA can be altered by certain chemical and physical factors. Such factors also cause mutations.

8. As stated earlier, genetic transformation can be brought about by introducing pure DNA into cells.

None of these pieces of evidence by itself is conclusive but, taken together, these evidences—the location of the DNA in the chromosomes, the correlation between the DNA content and the chromosomal constitution of the nucleus and other observations mentioned above-leave little doubt that DNA is the genetic material.

STRUCTURE OF DNA AND RNA

DNA is the key molecule in all biology. It is the most complex and the largest and the heaviest molecule of the living world with a molecular weight running into millions. It belongs to a class of compounds called polymers. Polymers are compounds formed of repeating units called monomers linked together. The monomeric units of DNA are compounds called nucleotides. Tens of thousands and even lakhs of these nucleotide units are joined to-

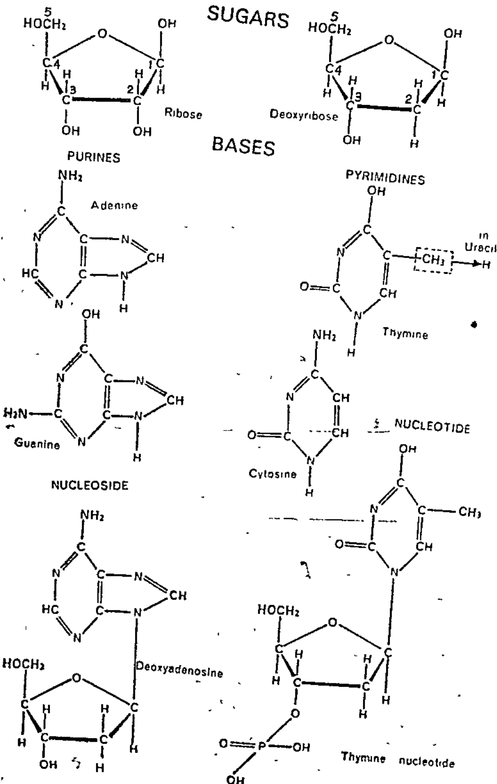


Fig. 11.2. Constituent of nucleic acids

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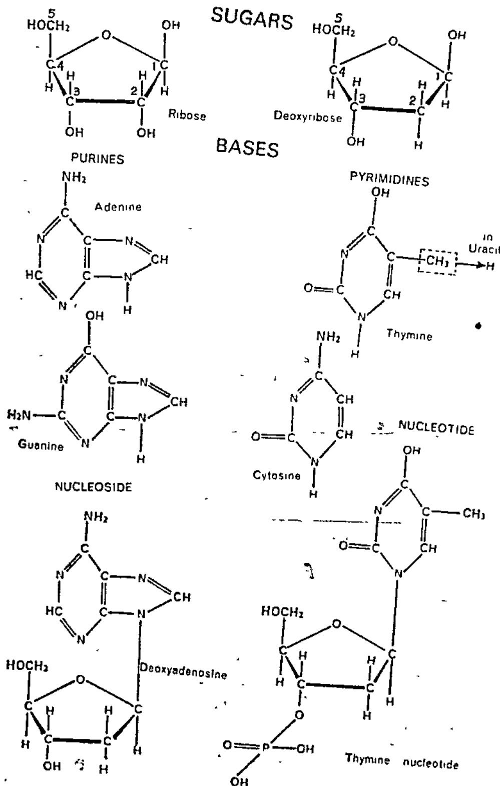


Fig. 11.2. Constituent of nucleic acids

gether in a specific manner to form a giant-sized macromolecule of DNA which is described as a polynucleotide. A nucleotide itself is a complex organic compound made up of three smaller molecules linked together. The smaller molecules are the pentose (5-carbon) sugar deoxyribose, phosphoric acid and one or the other of the four nitrogenous organic bases (Fig. 11.2). The common nitrogenous bases in DNA are adenine (A), guanine (G), thymine (T) and cytosine (C). The first two bases are purines and the last two are pyrimidines. The pyrimidines and purines are nitrogen-containing organic closed ring compounds. The former are six-membered ring compounds and in the latter a five-membered ring is joined to a pyrimidine ring. In the DNA molecule the sugar molecule deoxyribose is bound to a base molecule. This double combination is known as deoxyriboside and belongs to a general class of compounds called nucleosides. A phosphate ester of a deoxyriboside is called a deoxyribotide and belongs to a general class of compounds called nucleotides. The relationship between the various components of the DNA molecule mentioned above is illustrated in figure 11.3.

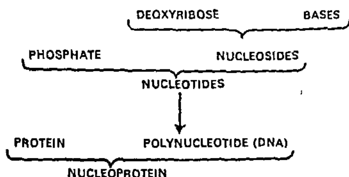


Fig. 11.3. Composition of DNA and the relationship of its various components

[illegible] molecule is always *linked* [illegible] phosphate group is also joined with the sugar molecule but in a different plane. The base and phosphate molecules are never linked *directly*. As there are four different nitrogen bases, there are four nucleosides and nucleotides in the DNA molecule. Their symbolic structures and names are given in figure 11.4. DNA is a polynucleotide (polymer) of these four monomeric nucleotides.

In the DNA molecule the four component nucleotide molecules are joined together by their phosphate groups. Tens of *thousands*

the long strands. The base molecules of the two strands are joined together by weak hydrogen bonds to form base pairs. Although

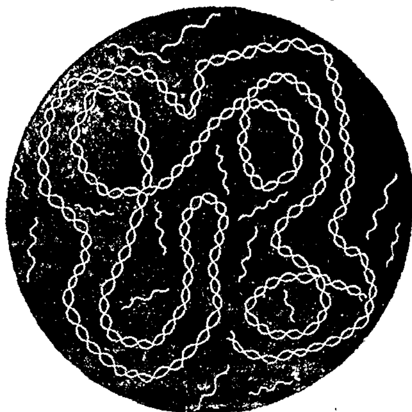


Fig 11.5. A single gigantic DNA molecule (double spiral) and small RNA molecules (single spiral)

the hydrogen bonds between the base pairs of the two strands are weak, their large number ensures that the two strands are held together by a fair degree of firmness. This arrangement gives to the DNA molecule a ladder-like appearance. The side rails or long banisters of the ladder which form the back-bone of the DNA supermolecule are formed by alternating sugar and phosphate groups bound by strong chemical bonds. The base pairs form the rungs or horizontal steps of the ladder. This ladder is, however, not straight. As conceived by J.D. Watson and F.H.C. Crick the two strands of the DNA molecule are twisted about each other at intervals around a central axis to form a double helix, *something like a spiral circular staircase (Fig. 11.6). There may* be thousands of turns in this spiral. The two strands of DNA travel in opposite directions. *In other words, they are of opposite* polarity.

The pairing between the bases is of a specific nature, a purine being always paired with a pyrimidine. Even the pairing between the purines and pyrimidines is specific. The purine adenine is always paired with the pyrimidine thymine by two hydrogen bonds and the purine guanine is always paired with the pyrimidine cytosine by three hydrogen bonds (fig. 11.7). This means that adenine is complementary to thymine and guanine is complementary to cytosine. Consequently, if the base sequence in one strand of DNA is known, *the sequence of bases in the other strand can be determined* because the two strands are complementary to each other. If at any point on one strand there is adenine, there is bound to be thymine *at the corresponding point* on the other strand. The total molar amount of adenine in any specimen of DNA is always equal to that of thymine (A=T) and the same 1 : 1 relation holds good between guanine and cytosine (G=C). As a corollary, it is also true that A+G=T+C. In other words, the total number of DNA purines is always equal to the total number of DNA pyrimidines. The DNAs of different species, however, show great variations in their A+T and G+C content. This is due to the fact that different specimens of DNA vary greatly in the types or frequencies of the bases present along the length of the molecule. They also differ in the sequence of base pairs along the great length of the DNA double

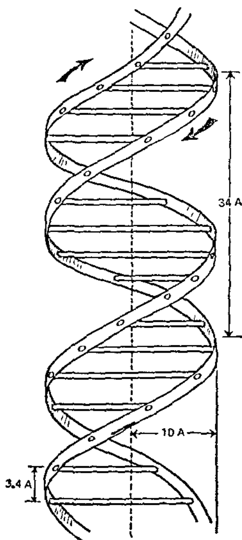


Fig. 11.6 Watson-Crick double helix model of DNA molecule

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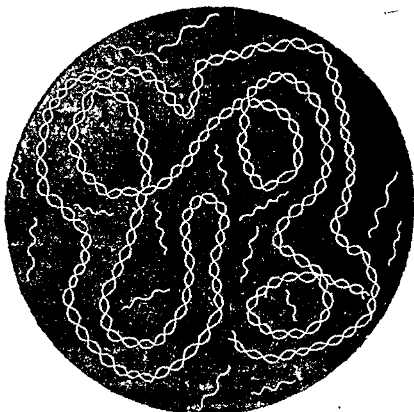


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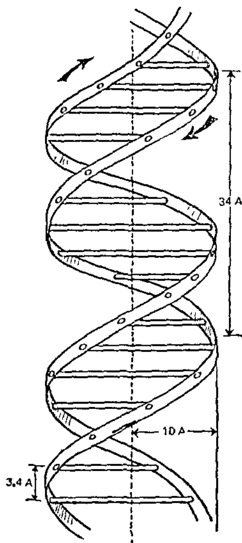


Fig. 11.6 Watson-Crick double helix model of DNA molecule

helix. The base pairs can be arranged in any sequence. The number of possible base sequences is equal to 4^n, where n equals the number of nucleotides per strand. This gives an infinite variety to the DNA molecule, each different for a different species. That is why we say that there are many kinds of DNA, each peculiar to a particular species. Each strand of the DNA molecule completes one spiral in a length of 34A (A=Angstrom=1/10,000 μ) and each complete spiral contains 10 base pairs. This means that each nucleotide occupies 3.4A along the length of a strand. The two strands have a diameter of about 20A (radius 10A).

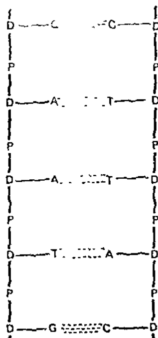


Fig. 11.7. A portion of the DNA molecule straightened out to show the arrangement of its various components and pairing of bases. D=deoxyribose

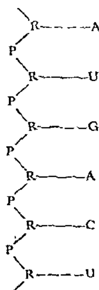


Fig 11.8. A portion of RNA molecule showing the linear arrangement of nucleotides. The sequence of bases has been selected at random. R=sugar ribose and Unitrogenous base uracil

RNA is the other nucleic acid. It is also a high molecular weight polynucleotide. It differs from the DNA in having the pentose sugar ribose in place of deoxyribose and in that the pyrimidine thymine is here replaced by uracil (Fig. 11.8). The other three bases are the same as in DNA. The nucleosides (combination of ribose and base molecules) of RNA are called ribosides and its nucleotides

are called ribotides. The RNA is, therefore, described as a polyribotide. The structure and terminology of the various ribosides and ribotides are given in figure 11.4. The various ribotides are joined together by their phosphate groups to form an unbranched linear chain containing hundreds of ribotide (nucleotide) units. The RNA molecule is a single-strand structure and not a double strand structure (Figs. 11.5 and 11.8). Its molecule is smaller and has a lower molecular weight than DNA. There are three kinds of RNA which play important roles in the translation of genetic information contained in DNA.

RNA is formed in the nucleus by the nuclear DNA. A part of it is present in the chromatin and nuclear ribosomes in the form of ribonucleoprotein (combination of RNA and protein). Most of it, however, is located in the cytoplasm, particularly in the cytoplasmic ribosomes. The RNA formed in the nucleus is stored in the nucleolus from where it passes out through the nuclear membrane into the cytoplasm.

REPLICATION OF DNA

An essential property of genes is self duplication or replication. DNA possesses this property. We have learnt that the two strands of the DNA molecule are complementary to each other. The first step in replication is the breaking of hydrogen bonds that bind together the two strands of DNA. The two strands thus separate from each other and unwind. Each strand then directs the synthesis of a new strand complementary to itself out of the free deoxyribonucleotides present in the environment of DNA. The deoxyribonucleotides, which are nucleoside phosphates, are first phosphorylated to produce energy-rich nucleoside triphosphates. The triphosphate molecules are later hydrolysed into deoxyribo?ide monophosphates (nucleotides) and pyrophosphates. This hydrolysis is accompanied by the release of energy which is utilised in binding together the nucleotide molecules to form a polynucleotide chain. In this process each strand acts as a model or template to which the free nucleotides are linked by hydrogen bonds with their complementary deoxyribonucleotides in the strand under the catalytic influence of the enzyme DNA polymerase. Thus an adenine base in the free nucleotide would pair with thymine in the DNA strand, a cytosine base in the free nucleotide with a guanine base in the DNA strand, and so on. This is followed by the formation of sugar-phosphate bonds between

successive nucleotides which arrive on the template (Fig. 11.10). The result would be that each single strand of the original DNA molecule would form a double stranded DNA molecule in which the new strand is complementary to and specified by the old strand. Further, the new strand that is added to an old DNA strand is equivalent to the other strand of the parental DNA molecules. Two daughter DNA molecules are thus formed which are identical to the parental molecule. It should be noted that every daughter molecule is half old, half new. Each daughter molecule contains one newly synthesised strand and one strand belongs to the old parental molecule which is entirely conserved (Fig. 11.9). For this reason the replication of DNA is described as semi-**conservative**. It may be noted that the breaking of the parental DNA molecule and the unwinding of the two strands occur in a small segment of the DNA molecule at a time. The synthesis of the new strands starts at one end of the old molecule and proceeds step by step to the other end. This property of replication of DNA is called **autocatalysis**.

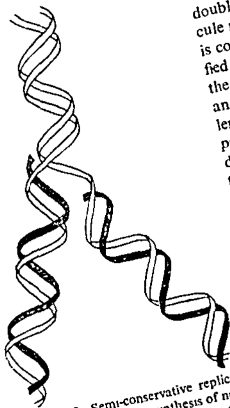


Fig 11.9. Semi-conservative replication of DNA. The synthesis of new strands (black) proceeds as the two old chains (white) unwind

NATURE OF THE GENE

A gene is a small segment of the DNA molecule. The length o the segment differs for different genes. Different genes differ in th number of nucleotides contained in the DNA strand in the ratio A : G, and also in the sequence of their nucleotides. Some ge are small and contain only a few hundred nucleotides while others their number runs into thousands. If we take 1,000 nucl tides as an average number for a gene, then a DNA strand

100,000 nucleotide pairs will contain 100 genes and one with 200,000 nucleotide pairs will contain 200 genes, each different on account of differences in the nucleotide sequence. In early cyto-

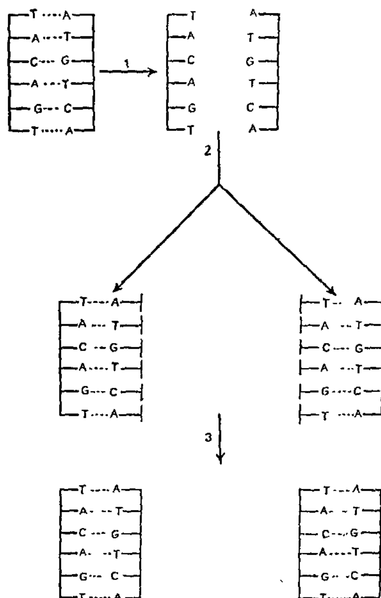


Fig. 11.10. The mechanism of DNA replication; 1, the separation of DNA double helix; 2, the assembling of free complementary nucleotides on the two DNA strands and their binding by hydrogen bonds; 3, the formation of sugar-phosphate linkages

logical studies, the chromosome looked like a string of beads or chromomeres. Later, when the salivary-gland chromosomes were discovered, the chromosome appeared to be made of dark bands alternating with light internodes. The chromomeres and the dark bands on the chromosomes described in chapter 6 are segments of DNA molecule which are densely coiled in a spiral manner like a coiled spring. The early cytologists regarded each chromomere or a dark band as a gene. The conception is still useful for many purposes, especially because it gives an idea of the linear arrangement of genes. Modern developments have shown that large gene units, like the chromomeres or bands, are made of smaller units. While formerly one gene was regarded as occupying one locus, now the same locus would be found to contain tens or perhaps hundreds of genetically different and distinguishable parts. The smallest hereditary unit is now thought to consist of a triplet of 3 nucleotides with an estimated length of about 10A or a millionth of a mm

HOW GENES FUNCTION

Most of the properties of living things are dependent upon their protein component. There are thousands of different kinds of cellular proteins. The great majority of them are enzymes which drive metabolic reactions. Almost ninety per cent of cellular proteins are enzymes. Cellular metabolism consists of an orderly sequence of reactions which take place in many steps. Each step is catalysed by a specific enzyme. The genes exercise their genetic function by controlling the synthesis of specific enzymes. Genes determine phenotypic traits by directing the course of metabolism through enzymic proteins whose synthesis is under their control.

In genetical language, a segment of DNA which contains the genetic information for the synthesis of one enzyme is called a **cistron**. A cistron contains from a few hundred to several thousand nucleotide pairs. The cistron is the nearest equivalent to the Mendelian gene. A gene then is a chain of several nucleotides of a DNA molecule which contains information for the synthesis of one enzymic protein. This is the '*one gene one enzyme*' hypothesis. The cistron is a functional unit of DNA. It functions as a gene. Any change in the structure of the cistron or in the sequence of its nucleotides will cause a change in the nature of the enzyme produced. This in turn will modify the sequence of metabolic reactions and ultimately the phenotype of the organism. Such a change in the cistron

constitutes mutation and gives rise to alleles. In chemical terms two alleles of a gene are two slightly different forms of a cistron.

In the Mendelian sense a gene was regarded as an indivisible unit comparable to the atom of physicists. This conventional concept needs to be revised. While the cistron, which is equivalent to a gene, is a functional unit, the smallest unit of mutation in DNA is a single nucleotide base and is called **muton**. The smallest indivisible unit of DNA, which is also a single base, which is capable of causing a change by recombination, is called a **recon**. Thus, the gene is not indivisible ; it contains smaller units, each a nucleotide base.

The relation between DNA and proteins becomes evident from the study of their structure. DNA is a linear polymer of specific nucleotides arranged in a specific order. Protein molecules are also polymers in which hundreds and thousands of amino-acids are joined together in a specific order to form a linear chain called polypeptides. The colinearity of nucleotide bases in the DNA and of amino-acids in the proteins is highly suggestive of relationship between the two. Sections of DNA with a specific nucleotide sequence determine the sequence of specific amino-acids in specific proteins. In other words, the blue print for the synthesis of specific proteins, each with a specific sequence of amino-acid units, is contained in the DNA.

RNA AND THE TRANSCRIPTION AND TRANSLATION OF GENETIC INFORMATION

There are some 20 different amino-acids which go to make up the thousands of different kinds of proteins. They are given in table 11.1.

A protein molecule contains 50 to several thousand amino-acid molecules (units) joined by peptide bonds. All or most of the 20 amino-acids may be present and arranged in a precise order which is peculiar to each specific protein. There are thousands of different kinds of proteins. They differ from one another in the relative content of the twenty odd constituent amino-acids and in the order in which the amino-acids are joined together in the chain. With twenty different amino-acid units to fill several hundred or thousand places, an infinite number of different proteins can be formed.

Although the number of different kinds of proteins is quite large, this number is really small as compared to the number of possible proteins that can be built out of the twenty or so constituent amino-acids. The reason why only a small number of such combinations is realised in the cell is that the synthesis of

proteins is under the genetic control of DNA which contains coded information for the sequence of amino-acids peculiar to each protein. A characteristic feature of the DNA giant molecule is the fixed content and sequence of nucleotide pairs along the entire length of its double helix. In this respect the DNA of any one species differs from the DNA of every other species. This genetic information for the synthesis of specific proteins is contained in coded form in the sequence of nucleotide bases along the strands of the DNA molecule. It has now been settled that a sequence of three bases in the DNA molecule contains the coded genetic information for one amino-acid. A triplet unit of this kind is called a **codon.** Each codon specifies only one amino-acid. With four different kinds of nitrogenous bases in the DNA nucleotides 64 different combinations of these bases are possible if they are taken three at a time. There are thus 64 codons (Table 11 2) The number of amino-acids which require coding is twenty. It follows that there are more than one codon for each of the twenty odd amino-acids. Such a genetic code is described as degenerate. The three bases in a codon may be identical *e g.* AAA, GGG, or all the three may be different, *e.g.* AGC, GAT, or a codon may have two different bases, one of the two occurring twice, *e.g.* AAG, AGA, AGG, GAG, etc.

The DNA is confined to the nucleus whereas the principal sites of protein synthesis are the cytoplasmic ribosomes. DNA does *not* move out into the cytoplasm. It exercises its remote control through another form of nucleic acid called RNA whose synthesis *it directs.* The DNA acts as a mould or template for assembling the right kinds of ribonucleotides (containing the sugar ribose) *into the right* kind of RNA. The ribonucleotides are present in the free state in the nucleoplasm in the form of riboside triphosphates. They arrive on the DNA template and are first hydrolysed into riboside monophosphates (ribonucleotides) and pyrophosphates. The ribonucleotide units are then linked together to form the *poly*-ribonucleotide strand of RNA in a manner described below. *Only one strand* of the DNA synthesizes the RNA. The systhesis of RNA is catalysed by a DNA-dependent enzyme, RNA polymerase. The enzyme breaks up the hydrogen bonds between the two strands of a section of the DNA double helix. The free ribonucleotides then pair with complementary nucleotides in one of the two DNA strands. As the enzyme moves forward the growing RNA strand peels off, and the two DNA strands *rejoin* by hydrogen bonds. In this process, the ribonucleotides are first

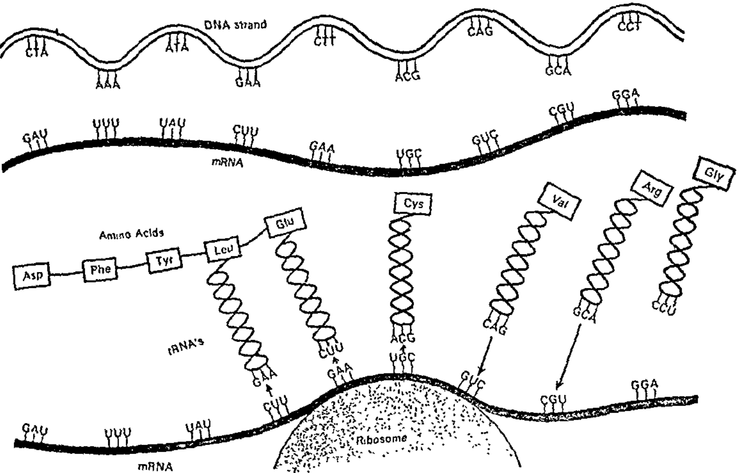


Fig. 11.11. A: the base sequence in the DNA strand and in its corresponding mRNA molecule; B, the mechanism by which amino acids are assembled at the ribosome-mRNA complex in a precise sequence to form specific polypeptides

converted into riboside triphosphates. These are later hydrolysed to produce the monophosphates and pyrophosphate molecules. The energy released during this hydrolysis is used for linking the ribonucleotide units (monophosphates) with one another to form polyribonucleotide strand of RNA. The base sequence in the single stranded RNA is complementary to the base sequence in the DNA strand which synthesizes it with the difference that the complementary base to the adenine of the DNA is uracil (and not thymine) in the RNA molecule. Thus adenine in the DNA is represented in the RNA by uracil, thymine by adenine, cytosine by guanine and guanine by cytosine as shown in figure 11.11. The genetic information contained in the DNA is now transferred to the mRNA. This is called **transcription** of the genetic information. The sequence of bases in the RNA contains the genetic information that was stored in the base sequence of its maker, the DNA. The genetic information now resides in the triplet codons of the RNA bases.

The RNA moves out into the cytoplasm to the site of protein synthesis. Because this RNA carries the coded information of the DNA to the cytoplasm, it is called **messenger** RNA (mRNA). The DNA is the director-general of genetic information which controls the working of the cell from its central office in the nucleus and mRNA is its working copy which goes out into the field and carries the instructions of its master, the DNA.

The mRNA molecule is very small as compared to the DNA molecule. Each mRNA molecule is formed by only a small segment of the DNA. As the DNA molecule is of great length it synthesises many mRNA molecules, each carrying complete genetic information for one specific kind of protein. There are many kinds of mRNA, each complementary to a particular segment of the parent DNA strand (cistron) and each specific for a particular kind of protein.*

A particular mRNA molecule which is specific for a protein containing 150 amino-acid units, arranged in a specific pattern, will contain 150 precisely arranged codons, each composed of three bases. This particular mRNA will contain a total of 450 bases and its approximate M.Wt. will be about 150,000. An mRNA molecule which specifies a protein containing 1,000 amino-acid units will contain 3,000 bases and will have a M.Wt. of about 1,000,000.

*For a detailed account of the chemical aspect of protein synthesis, readers are referred to "A Textbook of Plant Physiology," 11th edition, 1972 by the author, published by Atma Ram and Sons, Delhi-6.

This is the recognition site of the tRNA for its specific codon on the mRNA strand (Fig. 11 12). Each tRNA has its specific anti-codon which is complementary to some codon on the mRNA strand.

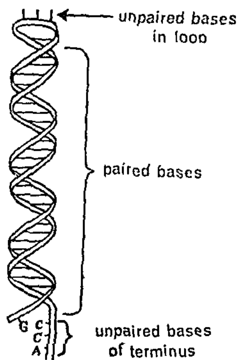


Fig. 11 12 Diagrammatic strucure of tRNA

Each tRNA has at its longer free end the base sequence –C–C–A. This is the recognition site of the tRNA for amino-acids. At this end each tRNA combines with its specific amino acid, forming a tRNA-amino acid complex. This is called the **adaptation** of the amino-acid and the tRNA is, therefore, also called the **adaptor** RNA. Before combining with its specific tRNA the amino acid is activated by adenosine triphosphate (ATP) and an *enzyme*. The tRNA–amino-acid complex then migrates to the mRNA – ribosome complex and attaches itself *to that particular site on* the mRNA which bears the codon to which its anticodon is complementary. Here it recognises the codon for which it is specific. Each tRNA is thus specific in two ways : *it is specific for a particular amino acid and it is also specific* for its particular codon on the mRNA. The ribosome moves along the length of the mRNA from one end to the other. In this way it becomes associated with different regions (segments) of the mRNA at different times. At any particular time only that region of the mRNA is operative which is associated with the ribosome. Each region on the mRNA chain carries a codon for its specific amino-acid. *Different regions become attached to different* tRNAs at different times. As a result of this attachment each tRNA delivers its specific amino-acid to a particular site on the mRNA chain, one at a time. *Thus, when at any particular time the ribosome is* in contact with the segment of mRNA which bears the codon GCU, then the tRNA molecule which has the anticodon CGA (this is complementary to the GCU codon)

will become attached to the mRNA at this point. This tRNA carries its specific amino-acid alanine. The amino acid is detached from the tRNA molecule and transferred to the mRNA chain at this point. The released tRNA moves back to the cytoplasm to pick up another alanine molecule. A tRNA may thus make many journeys to the ribosome. As the ribosome or ribosome group moves along the length of the mRNA in one direction from one end to the other each of the different codons borne on the mRNA strand will pick up its specific amino acid from the specific tRNA. Thus the several amino acids will become attached to different but specific segments of the mRNA one by one. The different amino acids are then joined to one another by peptide bonds one by one, forming a long polypeptide chain The sequence of amino acids in this chain is determined by the sequence of codons on the mRNA molecule. Each mRNA has enough length to contain a sufficient number of codons to synthesize a cellular protein as an open polypeptide chain. Thus, the ribosome-mRNA complex controls the synthesis of peptide bonds between the amino acids to form specific proteins, each having a specific sequence of the different amino acids along its polypeptide chain.

THE GENETIC CODE

The important question now is to determine which codon codes for which amino acid. There are some 20 amino acids and 64 codons. For each of the twenty amino acids there are, with one exception, 2 to 6 codons. The genetic code has been experimentally deciphered and perfected by Marshall Warren Nirenberg, Robert Holley and Hargobind Khorana who were awarded the Nobel Prize for 1968 for their work. The 20 amino acids and their mRNA codons are given in table 11 1. The 64 mRNA codons and their amino acid assignments are given in table 11.2. The amino acids are indicated by their abbreviations which are the same as in table 11.1. It will be noticed that the first two bases for the possible triplets for each amino acid are always the same. The third base can vary. In some cases it can be U, C, A or G but in most cases it can be either the pair U and C or the pair A and G. These relationships probably enable in some way the anticodon triplet in tRNA to recognise the codon triplet in mRNA.

Two of the mRNA triplets UAA and UAG do not code for any amino acid and were regarded as "non-sense" triplets. They have

TABLE 11 1.
Proteinogenic amino acids and their mRNA codons 1965

Amino Acid	Abbreviation	Codons: Common bases	Codons: Complete codons
1. Alanine	Ala	GC-	GCU GCC GCA GCG
2 Arginine	Arg	CG-	CGU CGA CGC CGG
		AG-	AGA AGG
3. Asparagine	Aspn	AA-	AAU AAC
4. Aspartic acid	Asp	GA-	GAU GAC
5. Cysteine	Cys	UG-	UGU UGC
6 Glutamine	GluN	CA-	CAA CAG
7. Glutamic acid	Glu	GA-	GAA GAG
8. Glycine	Gly	GG-	GGU GGC GGA GGG
9. Histidine	His	CA-	CAU CAC
10. Isoleucine	Ileu	AU-	AUU AUC AUA
11. Leucine	Leu	UU-	UUA UUG
		CU-	CUU CUC CUA CUG
12. Lysine	Lys	AA-	AAA AAG
13. Methionine	Met	AU-	AUG
14. Phenylalanine	Phe	UC-	UUU UUC
15. Proline	Pro	CC-	CCU CCC CCA CCG
16. Serine	Ser	UC-	UCU UCC UCA UCG
		AG-	AGU AGC
17. Threonine	Thr	AC-	ACU ACC ACA ACG
18. Tryptophan	Try	UG-	UGG
19. Tyrosine	Tyr	UA-	UAU UAC
20. Valine	Val	GU-	GUU GUC GUA GUG
Terminating triplets	Trm	UA-	UAA UAG UGA ?

Trm are the "end of message" triplets. ? a doubtful triplet

been found to be of "special sense". They are terminal codons which perform the significant function of terminating the code message. They serve to mark the boundaries of adjacent genes. In other words, they are gene separators or indicators of where one gene ends and another begins.

A nucleotide base forms part of *only one codon*. None of the three particular bases which make a codon forms part of *any other* codon. In other words, each base triplet is an independent unit. In genetic language such a code is described as **non overlapping**.

The DNA-RNA-protein code is universal to all living organisms, whether plants, animals or microorganisms. *It does not change* from species to species. The same particular code forms the same particular kind of protein in such diverse organisms as an ant, elephant or man, and in *Chlamydomonas* and a banyan tree. *Once* developed, it has not changed in the course of evolution. *In other* words, the code is a conservative one. The mRNA of one

species when introduced into an unrelated species will cause the ribosomes of the recipient species to make a protein characteristic of the donor species. This means that the mRNA of one species can be read by the protein-synthesizing machinery of another unrelated species.

TABLE 11 2
mRNA Genetic Code

FIRST LETTER	SECOND LETTER U	C	A	G	THIRD LETTER
U	UUU } Phe	UCU } Ser	UAU } Tyr	UGU } Cys	U
	UUC	UCC	UAC	UGC	C
	UUA } Leu	UCA	UAA } Trm	UGA ?	A
	UUG	UCG	UAG	UGG Try	G
C	CUU } Leu	CCU } Pro	CAU } His	CGU } Arg	U
	CUC	CCC	CAC	CGC	C
	CUA	CCA	CAA } GluN	CGA	A
	CUG	CCG	CAG	CGG	G
A	AUU } Ileu	ACU } Thr	AAU } AspN	AGU } Ser	U
	AUC	ACC	AAC	AGC	C
	AUA	ACA	AAA } Lys	AGA } Arg	A
	AUG Met	ACG	AAG	AGA	G
G	GUU } Val	GCU } Ala	GAU } Asp	GGU } Gly	U
	GUC	GCC	GAC	GGC	C
	GUA	GCA	GAA } Glu	GGA	A
	GUG	GCG	GAG	GGG	G

*Trm are the "end of message codons. ? is a doubtful triplet.

The property of DNA of synthesising enzymic proteins of specific structure which control cell metabolism is called **heterocatalysis** in contrast to its function of autocatalysis by which it produces a faithful copy of itself. Autocatalysis and heterocatalysis are the two important functions of DNA

Before closing this article, we may mention one more point. We have described cistron as a functional unit of DNA which codes for the synthesis of one protein molecule. It is the equivalent of the conventional Mendelian gene. Some protein molecules are very large and are made of several polypeptide chains linked together. Each peptide chain forms a constituent segment of the large protein molecule and its synthesis is under the genetic control of a separate cistron so that more than one cistron are involved in the synthesis of different constituents of the same protein molecule. In such cases the term gene should cover the whole group of linked cistrons.

A given gene is characterized by a fixed sequence of triplet codons. For each triplet of nucleotide bases there is a specific amino acid occupying a corresponding position in the polypeptide chain which the gene specifies. Thus, triplets on the left hand of the DNA polynucleotide will have corresponding amino acids on the left hand of the resulting polypeptide chain ; those on the right hand will have their corresponding amino acids on the right hand of the polypeptide and the triplets in the centre of the gene will have corresponding amino acids in the central position in the polypeptide. In short there is an exact colinearity between the sites of triplets in a gene and the sites of amino acids in the polypeptide, encoded by them

MOLECULAR BASIS OF MUTATION

A characteristic of the conventional Mendelian genes is their ability to undergo mutations. The mutations give rise to alleles. The different types of mutations have been described in chapter 10. These are point mutations and mutations resulting from structural changes in the chromosomes. The genetic material must provide a mechanism by which such mutations arise. Investigations in the last few years have demonstrated that the DNA molecule is the basis of gene mutations.

A DNA molecule is made up of four kinds of nucleotides arranged in a linear order. The genetic properties of a particular DNA molecule stem from the specific sequence of its nucleotide bases in its complementary strands. Change in this sequence at any site will cause mutation in the DNA molecule. Some of the methods by which mutations are produced in the DNA molecule are briefly described below :

Tautomerism. The normal pairings betw[illegible] DNA bases are A—T, T—A, G—C and [illegible] In e[illegible] four base

molecules shown in figure 11 2 the different atoms are arranged in a certain manner. Sometimes, a slight shift in this arrangement occurs as a result of an atom interchanging its position with another atom. The result is a changed form of the base. This phenomenon is called **tautomerism** and the changed forms of bases are called **tautomeric forms**. Tautomerism usually affects the =O (keto) or -NH_2 group of the base. The tautomeric form instead of forming hydrogen bonds with the usual complementary base forms an illegitimate pairing with a forbidden base. Let us illustrate this with an example. The normal form of the purine adenine (A) forms a base pair with the pyrimidine thymine (T). Its rare tautomeric form (A′) can pair with the pyrimidine cytosine. Similarly, a rare tautomeric form of cytosine (C′) can pair with adenine (A). A rare tautomer of thymine (T′) can pair with guanine (G) and the tautomeric form of guanine (G′) can combine with the normal form of thymine (T). The result in each case is an unusual purine-pyrimidine pairing as illustrated in figure 11.13 and summarised below :

Normal pairing	*Tautomeric pairing*
A—T	A′—C
C—G	C′—A
T—A	T′—G
G—C	G′—T

Fig 11.13 Tautomerism of the common bases of DNA and the unusual pairing of tautomeric bases (right side)

Such unusual pairings can be induced in bacteria and yeast by chemical mutagens like nitrous acid and can also occur spontaneously.

When a DNA molecule carrying a tautomeric base pair. A′—C for example, undergoes replication then C will form base pair with G in the daughter molecule giving rise to G—C pair at the site where originally A—T base pair occurred. The net result is the replacement of A by G. This is called **base-pair transition**. Such a change in a single nucleotide of the DNA molecule is equivalent to point mutation in the chromosome. One change of this type affects one codon. The changed triplet codon may then code for a different amino acid.

Tautomeric change affects only one of the two strands of the DNA molecule. As the DNA replication is semiconservative, the DNA strand containing the changed base will give rise to a

mutated daughter molecule while the other strand will produce the unmutated DNA molecule. The progacy will, therefore, be a mixture of mutated and unmutated DNA. The original DNA molecule in which one strand mutates in this manner is described as **mutational heteroduplex.**

Experiments on bacteria and bacteriophages (viruses which infect bacterial cells) show that base pair transitions resulting in point mutations are caused by 5-bromouracil (5 BU) which is a close analogue of thymine. When bacteria are grown on a medium containing 5BU and thymine is eliminated the result is that in all daughter DNA molecules 5BU occupies the positions normally occupied by thymine The bacterial cells, and the bacterophages that infect them, then show a higher rate of mutation. This mutagenic effect of 5 BU is due to the fact that 5BU has a higher frequency of tautomerism than thymine. Its tautomeric form then pairs with guanine, thus giving rise to G—C pair in place of A—T pair at the original site. Similar changes in the bases leading to the production of rare forms of bases are also produced by ionisation. In bacteria many purines and purine derivatives; e.g. 2-aminopurine (2AP), have been found to be mutagenic.

Rotational Substitution. In this the two bases of a pair break their bonds with sugar in the two strands and before rejoining rotate through 180°. Thus C—G becomes G—C and A—T becomes T—A. The result in each case is a mutation, due to change of a triplet at a particular site in each strand of the DNA. This is called **transversion.**

Breakage of the DNA Molecule. In the mutations described above no lengthwise breakage of the DNA strands is involved. However, sometimes, the phosphate-sugar backbone of the DNA molecule breaks at two points. A nucleotide pair or a whole group of them may be lost before the broken ends rejoin, giving rise to deletions of variable magnitude. Similar breakages may lead to addition of one or more nucleotides. Deletions have been induced by nitrous acid and by introducing radioactive phosphorus (p^{32}) in the DNA of bacteriophage particles. Mutations, depending upon deletions or additions, or both, of single base pairs or of a few base pairs have also been induced by a class of organic compounds called acridines. The mutant effect of the addition or deletion of a single nucleotide is illustrated in figure 11.14.

CAT | CAC | ACG | ATG | ACT	Normal sequence of triplets
CAG | TCA | CAC | GAT | GAC | T +	+mutation due to insertion of extra base G
CAT | –ACA | CGA | TGA | CT	–mutation due to deletion of a base C
CAG | T–AC | ACG | ATG | ACT	±recombinant

Fig. 11.14. The mutant effect of *addition* and *deletion* of a base

In both cases, there is alteration in the sequence of triplets in the cistron. If a base is added and another is deleted nearby most of the triplets remain unchanged. The first of the two mutations, in such cases is called the primary mutation and the second is called secondary mutation. The latter may compensate or suppress the effects of the primary mutation. When a deleted segment of a DNA molecule, containing one or more codons, is inserted in a break in the homologous DNA molecule (of the homologous chromosome), the result would be a duplication. Inversion or translocation to new positions with or without inversion have similar mutant effects. Inversions involve both the strands of DNA so that strand polarity may be maintained.

Manganese ions are strong mutagens. In their presence ribose and uracil may be added to a DNA strand, forming a compound DNA. When this strand is used as template it will pair with its complementary base (adenine), resulting in the addition of a new nucleotide pair to the compound DNA.

REGULATOR GENES

The genes (sections of DNA molecule) code for the synthesis of specific proteins through a transcription mechanism by which a specific mRNA is formed by each gene by virtue of the heterocatalytic function of the DNA. This should not give to the reader the impression that the function of all genes is to code for the synthesis of cellular proteins. The work of French scientists, Jacob and Monod, led to the recognition of two kinds of genes. Those that code for the synthesis of proteins are called structural genes. There are a large number of such genes which code for the synthesis of a great variety of cellular polypeptides. There is another class of genes which do not code for any protein. Their only function is to regulate the functioning of structural genes. They

are called **regulator genes.** They determine whether a structural

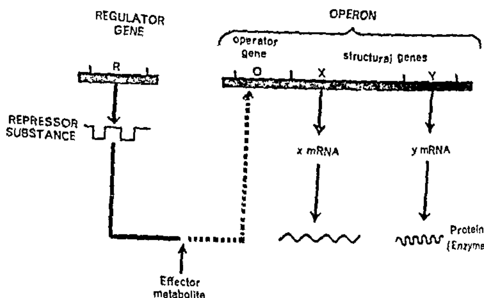


Fig. 11.15. Relationship between a regulator gene and operator and structural genes of an operon

gene will at any time and place function or not in the transcription process leading to the synthesis of proteins. Each cell of an organism contains all the structural genes. Yet, at any particular time, in certain cells a given structural gene does not produce the enzyme that it can. Similarly, a cell at certain times does not produce the enzyme in spite of the genes for it. Such cases point to the existence of a mechanism by which the heterocatalytic function of the structural genes is repressed. This mechanism is of the nature of regulator genes.

The regulator genes suppress the heterocatalytic function of structrual genes through some chemical substance present in the cell which is called the **repressor substance.** In the presence of the repressor the structural genes which are under the control of the regulator genes do not synthesise their characteristic mRNAs and their specific enzymes are not produced.

Under certain conditions the repressor substance is neutralised or inactivated by some chemical component of the cell. Such a substance is called the **inducer** or **effector.** It will remove the repressive effect of the regulator gene. In the presence of the effector the structural genes will synthesise their specific mRNAs, which in turn will set into operation the mechanism for the synthesis of enzymic proteins.

A regulator gene often controls the heterocatalytic function of a group of linked structural genes Quite often, it exercises its regulatory function through another kind of gene called the **operator** gene which is situated at one end of the group of structural genes (Fig. 11.15). The group of linked structural genes and the operator gene behave as a unit which has been given the name of **operon** by Jacob and Monod.

The operator gene acts as a switch mechanism for the entire group of structural genes with which it is associated. In the presence of the repressor substance the operator gene switches off its structural genes whose functioning is then stopped. When the effector substance is present the operator gene switches on the structural genes whose heterocatalytic function is set into motion.

The repressor is usually an amino acid which is toxic to the cell when present in large quantity. The regulator gene then represses the functioning of those genes which exercise a genetic control on the production of those enzymes which catalyse the synthesis of the toxic amino acid.

The inducer is often the natural substrate of the enzyme which it causes to be produced. In the absence of the substrate. the production of its enzyme would be a purposeless wastage of material and energy. The repression mechanism is a safeguard against this unnecessary wastage. It stops the production of the enzyme when it is not needed. When the substrate of the enzyme is present the inducing mechanism is switched on and the structural genes become active, resulting in the production of the enzyme which will act on the substrate. In other words, the activation or repression of the structural genes is related to the needs of the cell.

It must be clearly understood that regulator genes are distinct from the structural genes. A regulator gene may be located on a chromosome other than the one on which its operon is borne. The regulator genes in no way change the nature of the enzymes produced by the structural genes. They simply determine the conditions under which the structural genes will produce their enzymes. The regulator genes ensure the functioning of the structural genes when the enzymes that they code for are needed by the cell and stop their functioning when their enzymes are not needed or result in the accumulation of products that are toxic to the cell.

QUESTIONS

1. What evidence can you adduce to show that DNA is the genetic material.

2. What is DNA? Describe the structure of DNA molecule. What evidence is there to show that it is a two stranded structure?
3. Differentiate between DNA and RNA. Describe the role that the two perform in the cell
4. Describe the autocalalytic and heterocalalytic properties of DNA.
5. Describe the mechanism of DNA replication.
6 Define the term 'gene' in terms of its chemical and structural nature. How do genes produce their phenotypic effects?
7. What do you understand by transcription and translation of the genetic information contained in DNA? Describe the mechanism involved in these processes.
8. Describe the mechanism by which DNA controls the synthesis of cellular proteins.
9. Write an eassay on 'genetic code'.
10. Discuss the molecular basis of mutations. How are they produced?
11. Describe the mechanism by which the activity of genes is controlled.
12 Write notes on the following :
    (*i*) Semiconservative replication of DNA
    (*ii*) Degenerate Code
    (*iii*) Non-overlapping code
    (*iv*) Regulator genes.
    (*v*) Operon
    (*vi*) Cistron
    (*vii*) Tautomerism
    (*viii*) Nonsense codons

12

PLANT BREEDING—PRINCIPLES AND METHODS

THE science of genetics was born only at the beginning of this century. Yet, it has very greatly influenced mankind. One of the greatest benefits that it has bestowed on man lies in the application of its principles to the improvement of plants and animals of economic value to him.

Man has been cultivating useful plants since prehistoric times. Even more than 4,000 years back, the primitive man was growing several of our food plants like banana, date-palm, mango, apple, pear, onion, barley, wheat and rice and the fibre plants like flax and hemp. More than 2,000 years have passed since the Asians cultivated beet, carrot, garden pea, oats, rye and sugar-cane and that was long before civilisation dawned over Europe. The natives of the new world were cultivating maize, cotton, red pepper, tomato, potato, and sweet-potato long before Columbus discovered America.

Since the early days of plant cultivation no significant addition has been made to the list of cultivated plants but great improvement has been made in the economic plants already under cultivation. In fact, man has been attempting since prehistoric times to improve his crop plants. The principal method used by man in early days of agriculture was that of selection. It was known that plants showed great variability amongst themselves. Selection consisted in picking out plants with desirable traits. Using this method, Luther Burbank (1849—1926) succeeded in developing giant Shasta Daisy and stoneless plum.

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The method of selection as originally practised was at best a hit-or-miss method. There was no experimental basis to decide whether the variations selected were due to favourable environmental conditions or they were hereditary. Thus, a farmer may select a plant with desirable qualities only to find that few are transmitted to the progeny. In spite of these limitations, selection has resulted in the development of many valuable and famous varieties of plants, such as Leaming corn (maize), Red Fife wheat, Kalyan Sona wheat and various varieties of tobacco.

A real improvement in our economic plants can be brought about by improving their inborn qualities. This became possible only after knowledge of the laws and mechanism of the inheritance of characters was gained in the early decades of this century and the science of genetics was born.

Plant-breeding is now a scientific process and takes into account knowledge of cytogenetics and the genetic basis of variations which have been described earlier in this book.

Plant-breeding is concerned with the improvement of economic plants, increasing agricultural production, with the discovery of new varieties, and with the production of new plants of economic value. Plant-breeding is actively carried out in every country and in India, besides the Indian Agricultural Research Institute at Delhi, Central Potato Research Institute at Simla, Rice Research Institute at Cuttack and the Sugarcane Research Institute at Coimbatore, there are a number of Agricultural Universities and research stations in the states also.

OBJECTIVES OF PLANT BREEDING

The principal aim of the plant breeder is to combine in one variety as many of the desirable and economic characters as possible. Some of the improvements sought in plants are given below.

1. **Increased production.** Man depends for his food entirely on plants, directly or indirectly. Even milk, butter, eggs and meat that are obtained from animals are ultimately derived from plants because the animals that provide these articles of food feed upon plants or plant products. With increasing human population man's food requirements have also been increasing. Despite great improvements in the methods of agriculture, increased use of soil fertilisers, improved irrigation and increase in land area under cultivation, man is not producing enough food to meet the require-

Nipha D.4 of Bombay ; and 8-A, 9-D, C-518 and C-273, PV18 and Kalyan 227 (renamed Kalyan Sona) of Punjab. C-273 yielded on average 973 Kgm of grain per acre. Using the new variety Kalyan Sona, a Delhi farmer obtained an all world record of 84·3 quintals per hectare (91·4 mds. per acre) in 1967. Recently, an improved variety C-306 has been evolved at Ludhiana. The new variety is a bearded wheat with white straw and grows well even under "barani" and late sowing conditions. Pb. 7 is a high yielding variety of gram. Similarly, a new sugar cane variety with 22% sugar content has been recently produced at Coimbatore. Another outstanding example of the achievement of plant breeding work in recent times is the high-yielding and protein-rich hybrid fodder crop NB.21 evolved by Dr. V.P. Gupta at the Punjab Agricultural University, Ludhiana. In general, it is one of the objects of plant breeding to evolve high yielding varieties of all crops. The case of hybrid corn has already been described in an earlier chapter.

The efforts of our plant breeders in the evolution of high yielding varieties of major food and fodder crops have been rewarded with remarkable success. The progress has been most spectacular in the case of wheat In 1965 we were producing about 12 million tons of wheat in a year. In 1970 the production exceeded 20 million tons. Increased cultivation of new wheat varieties has brought about a green revolution in the country. Much improvement has also been achieved in crops like maize and rice but a complete break through of the magnitude achieved with wheat has yet to be achieved in these crop plants and others like bajra, jowar, pulses oilseeds and cotton. All the same, India has now achieved self-sufficiency in food, saving much valuable foreign exchange. Food production in 1969-70 reached an all time record of 100 million tons. The nation bows its head in gratitude to its scientists who deserve full marks for their work and achievements. If our politicians steal the credit for this, it cannot be helped under the present set-up While our politicians are fighting for power, it is the plant breeders and other scientists to whom the people must look for the solution of their food and other problems. These men deserve greater admiration and consideration than they get. They are more important to the nation than the whole lot of politicians, most of whom are more concerned with their personal ambitions for power and patronage It would be a good day indeed for the country when our people discarded the professional politician and placed their destiny in the hands of scientists and technocrats.

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2. Improved quality. The qualities which matter vary in different plants. Garden plants are prized for their shapeliness, density, size, brighter colour and colour patterns ; shape of the inflorescence and better spacing of the flowers , earlier flowering, late flowering, longer flowering, etc. Fruits are valued for their colour, size, shapeliness, amount of juice, taste, flavour and higher mineral and vitamin content. Crop plants are valued for their yield, resistance to frost, drought, lodging and disease, nutritional value etc.

A few examples may be described to illustrate the point The original sugar beet varieties cultivated about the end of the eighteenth century yielded less than 7 per cent sugar and were not suitable for sugar manufacture. Lately, varieties capable of yielding 15 to 18 per cent sugar have been developed so that sugar beet is now an important source of table sugar. Wheat varieties are valued in India for their milling, baking and chapati-making properties, their grain colour and protein content. The high yielding imported varieties of Mexican wheat are red grained and are not suitable for making chapatis. From this parental stock improved varieties, for example Kalyan Sona, have been developed which bear amber-coloured grain and make tastier chapatis. Another variety Sharbati Sonora has been produced at the I.A.R.I. from the red-grained Sonora-64 by mutation with gamma irradiation. This variety is hard, amber-coloured and is richer in protein content than the parent.

An excellent example of improvement in quality resulting from hybridisation is cotton. The most valuable fibre plant known is the variety of "long staple" cotton. It was produced by hybridising two well-known varieties of Egyptian cotton. G-24 is an Indian variety of gram which gives 'high yield' but the colour of grain is dark brown, an undesirable character. This variety has been crossed with Pb. 7, I. P. 58 and G.17 to improve its colour. The result is C132 which gives higher yield at Ferozepore and C158 which proved better for Rohtak district in Haryana.

3. Resistance to disease and insect pests. Plants are subject to the ravages of diseases. A field of wheat may be decimated by black stem rust ; or thousands of sugar-cane plants may be affected by red rot. Such and a host of other diseases, caused by fungi, bacteria or virus result in great loss to the farmer , and sometimes cause untold misery to the people. Potato blight caused by the fungus *phytophthora infestans* was responsible for the famous potato famine in Europe in 1945-47. In Ireland, where potato is the main

article of diet, the entire crop failed, resulting in famine and untold suffering. Thousands of people died of starvation and several thousands of Irish people emigrated to the United States. Breeding of strains resistant to diseases has, therefore, become an urgent necessity. Resistance to disease is often the only quality for which a variety is grown. Considerable efforts are accordingly made to develop varieties which are immune to disease, wheat immune to rust, potatoes immune to blight, tomatoes immune to wilt.

In a number of cases, the efforts of geneticists have met with success in this direction but much yet remains to be achieved. The cultivation of rust resistant wheats, *e.g.*, has been attended with spectacular benefits. It makes all the difference between a good harvest and crop failure. While it ensures a reasonable harvest to the farmer it is also of importance to the nation. Sharbati wheat of Madhya Pradesh is rust resistant. C 250, C 253 and C 228 are the wheat varieties that are highly resistant to yellow rust but not to black rust. The breeding of wheat varieties which combine high productivity, good milling and baking properties and resistance to rust and smut diseases is an ideal deserving of persistent and concerted efforts. Gram varieties G. 24 and G. 17 have been evolved as resistant to gram wilt in the Punjab; C 235 has been evolved as a blight resistant cross and is sown in blight affected humid areas.

plums with the wild plums of the region and selecting the best of the resulting hybrids. Similarly, wheat, barley, oats and rye have all had their areas of cultivation extended by the production of new varieties.

5. Varieties resistant to lodging. High yielding crop plants have a tendency to lodge under conditions of increased irrigation or greater application of fertilisers. This adversely affects the quality and quantity of plant products. Resistance to lodging is a desirable character in crop plants A noteworthy example is the Mexican dwarf wheat which is highly responsive to high levels of fertilisation and is resistant to lodging.

6. Novel varieties. One should always be on the lookout for new varieties. Novelty has its own charm and value. A new kind of mango and a new flower colour is sure to be patronised, and some of the new varieties may prove to be superior to the old in one respect or the other.

THE ART OF PLANT BREEDING

Plant breeding is a long and slow process. It involves many operations and procedures, and requires technical knowledge and skill. Plant breeding is both an art and a science. Every plant breeding programme must take into account the method by which the plant in question propagates, because the plant breeding methods are related to the reproductive systems. Some species propagate asexually by vegetative structures and others sexually by seeds. The plants in the latter group fall into three categories ; those that are self-pollinated, those that are cross-pollinated, and others in which both self- and cross-pollination occur. Self-pollination tends to produce a homozygous population and cross-pollination makes the natural population heterozygous. In crop plants, in which both types of pollination occur, the population consists of a mixture of homozygous and heterozygous forms. Many of the asexually propagated crop plants are heterozygous for many factors. Vegetative propagation maintains this heterozygosity because no segregation of heterozygous factors can take place during mitosis which alone occurs in vegetative reproduction to the exclusion of meiosis.

In vegetative propagation, therefore, the population becomes uniform or homogeneous though it may be heterozygous. The characters that are homozygous continue that way and further production of heterozygous condition is also prevented. For selection

in vegetatively propagated crops it is necessary to induce the production of seed by the sexual method. As a result of accompanying segregation and recombination new and large variations are thrown out. These variations provide the material for the selection of desirable types. These selected types are then propagated vegetatively to obtain a homogeneous population.

Before describing the methods, used for the breeding of different kinds of crop plants we will briefly deal with the various subjects which have a bearing on plant breeding.

ROLE OF VARIATION IN PLANT BREEDING

Careful selection is an important operation in all breeding programmes. Selection presupposes the occurrence of variation in nature. Variability is inherent in the plants and is the basis of plant breeding. But for this, no improvement in our cultivated plants could have been possible It is this variability that has made our cultivated plants very different from their wild ancestors. Besides recombinations dependent upon meiosis and crossing over, the principal methods by which natural variations arise in crop plants are : (1) 'Mendelian variations,' (2) interspecific hybridisation, and (3) polyploidy.

1. **Mendelian variations.** These originate primarily by gene mutations. When different alleles of a gene come together as a result of hybridisation the result is the production of further diversity in the population of a species. Sometimes, a single mutation may produce drastic or manifold effects. Some of these mutational changes in a species may be preserved by man by artificial selection because they are useful to him. Cabbage, cauliflower and kohlrabi have been derived form the wild cabbage in this manner.

Mutations result in the accumulation of a store of diversity. The desirable variations are then preserved by selection. In this way are produced varieties that are suitable for different purposes and adapted to different conditions.

2. **Interspecific hybridisation.** Sometimes, hybridisation between distinct varieties or species followed by segregation results in the production of improved types. These types are pronounced heterozygotes and do not breed true. These are then preserved by the vegetative methods of propagation like budding and grafting. Certain varieties of pears, plums, cherries and grapes and many garden plants such as certain roses and lilies arose in this manner.

3. **Polyploidy.** The different types of polyploidy and their role

in the origin of new types of plants have been dealt with in chapter 10. The simplest autopolyploids are triploids. Triploids are highly sterile on account of the unbalanced chromosome sets and are, therefore, propagated asexually. Some of the commercially important varieties of apples, pears, grapes, oranges, guava and pineapples are triploids and are propagated vegetatively. The common bananas also belong to this category and have 33 chromosomes as compared to the 22 chromosomes of ordinary diploid varieties. The fruits are seedless and the triploids are characterised by increased vigour and size of plant and fruit. A triploid tea and a triploid mulberry are cultivated in Japan and are popular because of their resistance to cold. Similarly, triploid water melons are widely cultivated in that country. The fruits are large and seedless and the plants are high yielders and wilt-resistant.

The white potato is a tetraploid with 48 chromosomes (2N=24). It is predominantly an autotetraploid but it appears to have been complicated to some extent with hybrid polyploidy.

More than half of the cultivated plants are allopolyploids, having arisen by hybridisation between closely related but distinct species followed by chromosome doubling American long staple cotton, tobacco, and wheat arose in this manner.

PLANT INTRODUCTION

Greater the variability the better are the results of selection. The local population of a species may not contain all the variability or even much of it. For best results it is often desirable to introduce new material from other tracts or from other parts of the world to tap all the possible sources of variation in the species. The introduced material must consist of a random mixture of many different types so that some of them may be able to acclimatise and establish in the new environment. Some of these excel the local population in performance and others give poor results and are ignored. Mixtures of heterozygous types give better results than pure lines. The segregation of the former produces types in which acclimatisation may improve or break down. Squashes, pumpkins, chillies, castors and sorghums are examples of crop plants introduced in India in the long past. Crop plants introduced in comparatively recent times include potato, tobacco, American and Cambodian cotton, rubber, coffee, tea, cashewnut, groundnut and maize. Among the latest introductions are soyabeen from China, high-yielding dwarf varieties of wheat from Maxico and the TN-variety of rice from Formosa and J. R-8 from the Philippines.

Introduction has played a significant role in the development of agriculture throughout the world. Wherever man has gone, he has carried with him the plants of his native land and has brought back home plants from distant lands. With the discovery of Americas, potato, maize and tobacco were introduced into Europe and other parts of the old world. Similarly, several crop plants were introduced into America by the colonisers and settlers from the old world. These include wheat, barley and sorghums from Asia Minor, oats from Asia Minor and North Africa, soyabeans from China and, in recent times, the Kharkov variety of wheat from Russia.

Introduction helps in the development of new varieties in three different ways : (1) directly from the introduced stock, (2) from selections from the introduced material, and (3) from hybrid offspring of introductions crossed with adapted native varieties. Well-known recent examples under No. 1 above are the rice strains 'Taichung Native-1' introduced from Formosa and I.R-8 introduced from the Philippines, and the wheat varieties Lerma Rojo and Sonora 64 introduced from Mexico. Under No. 2 above are several wheat varieties evolved by selection from the imported Mexican wheat. Sona-227, Saphed Lerma and Sonalika produced at the Indian Agricultural Research Institute (IARI) and PV-18 and Kalyan-227 evolved at the Punjab Agricultural University, Ludhiana, are examples of wheat strains developed by selection from this variable parental stock. Under No. 3 above may be cited the several imported inbred lines of American maize used as parents in the production of hybrid varieties of maize. Similarly, the dwarf Mexican wheat has been crossed to the tall variety of Indian wheat with the object of transferring the genes determining the lodging-resistance of the former to the tall Indian variety.

The Russian agrobiologists have exploited the principle of introduction fully. They sent exploration expeditions to several parts of the world and collected some thousands of new varieties of crop plants. When introduced on Russian soil, several of them gave better performance than the native varieties. *It is possible that selection may bring out a variety which in nature combines all the economic characters desired by man.*

As a result of these explorations Nikoli Ivanovitch Vavilov, world's greatest authority on the dispersal of crop plants and their relatives, came to the conclusion that the greatest diversity in a species is to be found in the centres of its origin. According to him there were eight great centres of origin of most of our crop plants

and the greatest diversity was to be found in these centres, namely China, India, Central Asia, Asia Minor, the Mediterranean region, Abyssinia, Central America, and west-central South America. These areas are now well-known fertile collecting areas and remain promising areas for future explorations. Vavilov also recognised secondary centres of origin and pointed out that valuable forms are found far removed from the primary area of origin Thus, the Navel orange was discovered in Brazil but its primary centre of origin was South-Eastern Asia.

SELECTION

Selection is an important and essential operation in all breeding programmes and has been practised by man since the early days of agriculture. In the pre-Mendelian period selection was based entirely on phenotype. Nothing was then known about the genotype. The selected types, being mostly heterozygous, did not breed true and quite often a rapid deterioration of quality occurred in the progeny as a result of segregation. New selection had, therefore, to be made for every sowing. Moreover, the apparently superior phenotype of the selected plants in many cases was due to favourable environmental conditions and had no genetic basis. Selection as practised now is a scientific process, based on the knowledge of genetics and cytology and aims at isolating superior genotypes.

The crop plants growing in the farmer's field are a heterogeneous population, consisting of several types that differ from one another both phenotypically and genotypically. Selection consists in picking out the better types and separating them from the inferior ones and favouring their perpetuation by reproduction under controlled conditions. There are two principal patterns of selection, namely **single plant selection** and **mass selection.** The only difference between these *two methods lies in the number of plants selected to* produce the progeny.

1. Single Plant or Pure Line Selection. Several single plants out of the variable population are selected which are superior with reference to the desired trait or traits. Thus, single plants not affected by a disease which is prevailing in the field are selected or plants may be selected for bearing the heaviest or largest number of grains in an ear or because they possess a certain quality not shown by the other plants. Selection should be for as large a number of plants as possible. Seeds from each selected plant are sown in separate rows to produce a progeny in which single

plant selection is again made for the desired character. Seeds from these selected plants are again sown separately. Selection is continued for several generations. In each generation the inferior and defective types are eliminated and finally a few superior types are selected which show outstanding performance and are found on comparison to be superior to the original field bulk. The entire procedure takes seven to ten years.

This method has led to great improvement in many crop plants. The most outstanding examples in recent times are the wheat varieties PV18 and Kalyan 227 developed at Ludhiana by selection from the variable wheat stock imported from Mexico.

2. Mass Selection. In this, many similarly appearing plants, rather than one, are selected for the desired trait and harvested. The seed from all the selected plants is mixed together to form a composite bulk which is known as mass selection. The mixture of seeds so obtained is used for raising the new crop. This kind of selection is based on phenotype and no progeny testing, as is done in single plant selection, is required. Selection may be repeated in the next and subsequent generations until it no longer produces results. The selected varieties developed by this method possess fewer genotypes than the original field population but more than the "single" genotype of varieties developed by the single plant selection. Its object is to purify the seed by the elimination of the inferior types and to improve the general level of the population by selecting and bulking the superior genotypes already present.

It must be noted that selection brings about a preferential perpetuation of certain characters, and, therefore, genes and the gradual elimination of other genes. The characters selected by man may not have any survival value to the plant. Thus, it comes about that in some cases artificial selection by man operates in a direction that is opposed to natural selection and results in the preservation and perpetuation of genes which, if left to themselves, would be gradually wiped out in natural selection.

HYBRIDISATION AND SELECTION

Selection, by itself, cannot bring out anything which is not already in the genes. It only helps to isolate the "good" genes but itself can never make the genes better. Even the best selected plants may have undesirable traits hidden as recessives and these are bound to come out in later generations. Further improvement is then made by hybridisation. Selection, as already stated, depends

on the occurrence of variability in the plants. Natural population of a species is a mixture of many different types. The useful variations are often scattered in different races or strains or species. The plant breeder aims at bringing together in one variety or race as many of the economically valuable traits as possible. This is achieved through hybridisation. Hybridisation means the crossing of two plants which differ from each other genotypically in one or more traits. The plants that are crossed may belong to the same species (intraspecific hybridisation), or to different species of the same genus (interspecific hybridisation), or to different genera (intergeneric hybridisation) A reference to the results of a dihybrid cross illustrated in figures 3·6 and 3·8 would show that two entirely new combinations of characters appear in some members of the F_2 generation. Hybridisation may thus lead to the production of new varieties by bringing together the best genes of two or more individuals, varieties or even species. To take an example, suppose it is desired in the case of wheat to combine the productiveness of one variety and rust-resistance of another in one true-breeding strain. True breeding selected plants of the two varieties are crossed with each other. The hybrid grains are then sown and the F_1 plants are selfed to raise an F_2 generation. This will consist of a variety of forms, some productive but not rust-resistant; others less productive but rust-resistant; others neither productive nor rust-resistant; and still others that are both productive and rust-resistant. Plants of the last variety are picked out and selfed. Selection is repeated in the next generation and the plants that breed true for both the characters are finally selected for seed production. Some of the most valuable crop varieties have been obtained by selection among hybrid progenies obtained from two or several less valuable varieties.

Two examples of the current breeding work being done in this direction at the Indian Agricultural Research Institute, New Delhi, may be cited here. The dwarf Mexican variety of wheat is resistant to lodging. Hybrid seeds have been produced at the I.A.R.I. by transferring the genes for dwarfness (hence its lodging-resistance) of the Mexican wheat to the tall varieties of Indian wheat. Some of the selected hybrid seeds are in the final stage of laboratory tests and are likely to be released next year. Similar hybridisation experiments are in progress with a view to developing hybrid varieties of rice which combine the high-yielding qualities of the Formosa-bred "Taichung Native-1" variety and the flavour and taste of the popular Indian Basmati variety.

Another illustration of this point may be given fro of East and Jones on tobacoo varieties used as tobacco The Sumatra and the broad leaf varieties were common neither satisfied the requirements of an ideal wrapper. leaf variety has a large leaf, a desirable trait, but a an undesirabletrait. The Sumatra variety has a good rour the leaf is small. The ideal leaf would be both large an East and Jones crossed these two varieties. Then by se several generations they established a new variety, the This variety has the good qualities of the two original It has large round leaves.

Recombination of characters is also brought about w meiosis a random interchange of genes or blocs of g place between homologous chromosomes as a result o over. This recombination potential, which varies very w species to species, is of great significance in plant breedir it releases new variability. By manipulating this vari selection, a skilled plant breeder can take long strides in ment of his objective of breeding superior varieties po combination of several useful characters. It would be sexual reproduction, while it is a source of variation in p also provides a mechanism for the recombination of v interbreeding populations. This variation provides the pla with the raw material out of which he can build new var

Many of the economic characters of crop plants are th interaction of many genes scattered over several chr Hybridisation helps to bring together these multiple f concentrate them in one variety.

Sometimes good results follow when two different s crossed. This is illustrated by the hybrid fodder grass, Pu which was evolved at the I.A.R.I. New Delhi, by cr Napier or the Elephant grass of Tropical Africa with Bajra. The New hybrid has 5% more proteins, 12% n and gives higher yield than Napier. It needs much less Napier and is very responsive to chemical fertilisers. A Napier-Bajra hybrid, NB 21, has been evolved by Dr. Ludhiana. It far surpasses Pusa Napier in per hectare yie

It must be clearly understood that hybridisation and create no new genes but only produce new combinations already present in the *parent stock*. When the parent more than two genes, a greater variety of recombination

will be obtained. With the help of this technique, numerous improved varieties of crop plants have been developed. There is still much scope for greater improvement in this direction. With the enormous knowledge of cytogenetics gained in recent years it is possible to produce plants to order. The plant breeder sets before himself an ideal and proceeds with breeding experiments, to realise his ideal as nearly as possible by combining the genes from two or more plants. In this process even the genes contained in wild plants are also considered. In this way is obtained a combination of several desirable characters in one variety, for example, high yield, better quality and resistance to drought or disease.

THE TECHNIQUE OF HYBRIDISATION

Practical hybridisation is a technical operation and requires skilled hands. The various steps involved in this process are briefly described below.

The first step is the selection of plants that are to be used as parents. The breeder must keep in his mind the objective that he wishes to achieve and select the parents accordingly. Only the best looking and vigorous plants that possess the desired characters are selected. Thus, he selects the one that bears the largest strawberries, or a wheat plant that bears the longest ear or one that bears the plumpest grain. He then marks the plants that are to be used as pollen parents and those that are to serve as the ovule parents. If the flowers are hermaphrodite, the stamens are cut off with the help of a pair of forceps or scissors from the flowers which have been earmarked as ovule parents. This operation is called **emasculation** and is carried out before the dehiscence of the anthers or the opening of the flowers, whichever is earlier. Other methods employed to achieve emasculation consist in subjecting the pollen to unfavourable environmental conditions like heat, cold or exposure to chemicals such as alcohol. In *Sorghum*, emasculation is carried out by dipping the panicle in hot water at 50°C for 10 minutes. This kills the pollen-grains. Recently, male sterility genes have been discovered and found effective in producing genetic emasculation. Emasculation is necessary, for otherwise self-pollination will take place and interfere with the results of cross-fertilisation.

In plants that bear unisexual flowers, the pistillate flowers are enclosed in paper bags, so that no foreign pollen falls on the stigma. This should be done before the stigma matures and becomes receptive. The staminate flowers should also be enclosed in paper bags

to prevent contamination by stray pollen from other plants. The male parents that are selected should be such that their time of ripening and dehiscence of anthers coincides with the time of ripening of the stigmas of the female parent.

The next step is the collection of the anthers from the male parent. This is done a short time after the dehiscence of anthers. The dehisced anthers are cut off from the filaments and collected in bags of fine muslin. The pollen from this collection is then dusted on to the stigma. This artificial transfer of pollen may be carried out with the help of a fine brush. In *Sorghum*, cross-pollination is brought about by enclosing the panicles of the male and female parents in the same bag and leaving them for natural cross-pollination. When the pollination has been effected the stigma is sealed off by a paper bag so long as it is receptive. Other methods, such as isolation in space, are also used for preventing chance natural pollination.

The seeds or grains are then allowed to set and collected when mature. They are stored separately and in proper season sown to raise the F_1 generation. The F_1 plants are self-pollinated to produce the F_2 generation which should be a very large one, consisting of several thousand plants. A large progeny is necessary so that all the possible combinations come out. Selections of outstanding plants, showing the desired combination, are made and from them the F_3 is raised in which selection is again made. This is repeated till about the F_6 generation. Sometimes, the selected F_2 is back-crossed with either parent. Selection is continued till the desired combination becomes homozygous and true breeding types are obtained.

This method has been rewarded with great success in many crop plants. Hybrid varieties of sugar-cane developed at the Coimbatore Research Institute are now famous the world over and are grown in Africa, America, East Asia, China and Australia. In rice, yield has been combined with strength of straw, and yield with resistance to paddy blast. Varieties of cotton combining yield with lint quality have been developed.

BREEDING OF SELF-POLLINATED CROPS

Most of the cultivated plants, the cereals, garden plants and vegetables are self-pollinated. Among the important self-pollinated crop plants are wheat, oats, barley, rice, sorghums, cotton, tobacco, potatoes, tomatoes, flax, sweet pea, soyabeans, peas and beans, and the fruit trees, apricot, peach and citrus.

The following breeding methods are employed in the case of self-fertilised crop plants and have been attended with considerable success :

1. Pure-line selection
2. Mass selection
3. Hybridisation and selection
   (*a*) Pedigree method
   (*b*) Bulk method
4. Multiple crossing
5. Backcross method

1. Pure Line or Single Plant Selection. As stated earlier in this chapter, this method consists in selecting single plants from the variable population in the farmer's field. Selection should be as large as possible.

The second step consists in sowing seeds from each selected plant in a separate row to grow the next generation and single plant selections are again made for the desired character. This is repeated for several generations and in each generation the performance of the selected plants under different environmental conditions is studied. In each generation, inferior and defective types, such as early or late types or disease susceptible types, are discarded and the number of selected types gradually goes on diminishing.

In the third and final step the residual selected types are compared with each other and with the common commercial varieties in the matter of yield or other characters for which selection is being made. These evaluation trials take about three years. Those types which give the best performance and are superior to the field bulk are finally selected and released as improved strains. The entire procedure is completed in seven to ten years.

Single plant selection in natural population has resulted in the isolation of many useful and improved strains in several crop plants, such as rice, great millet, pearl millet, ragi, cotton, etc. Many varieties of crop plants resistant to disease have been discovered by this method when one or more plants of a crop happened to be immune to a disease that prevailed in an epidemic form among cultivated plants. Thus, in Tirak-attacked cotton single plant selection brought out a strain that was resistant to this disease.

In self-fertilised plants, this technique results in the isolation of true breeding strains or pure lines. Self-fertilisation in nature [illegible] segregation of heterozygous factors and brings about hom[illegible]

in plants. The population of a naturally self-fertilised plant like wheat or bean thus comes to consist of several homozygous forms, each breeding true. In other words, population is homozygous but heterogeneous. As a result of selection in such a population the several homozygous forms or pure lines get separated from one another. Each line is now a distinct strain with reference to the trait or traits for which selection is made. Within a pure line the population is homogeneous. Such a pure line is free from any genetic variability and, further selection within it has no effect. This is because the progeny of a homozygote (*AABB*) will have the same genotype (*AABB*) as the parent. This may be summed up by saying that selection cannot lead to improvement in a pure line. This was shown by a Danish botanist Johannsen (1903) as a result of his classical experiments on the bean plant. This plant is self-fertilised in nature. By the single plant selection Johannsen isolated 19 pure lines of bean as regards mean weight of the seeds. In the pure line strain number 15 the mean weight of the beans was 45·0 cgms Some beans in the pods of this strain weighed only 20 cgms; some 50 cgms; and others 60 cgms. Plants grown from these three kinds of beans showed the mean weight of the beans produced on them to be respectively 46·9, 44·6 and 45·0 cgms. This shows that within a pure line the variations in the weight of the individual beans were due to difference in their environment and nutrition. There was no genetic variation among them and, therefore, their breeding behaviour was the same. In this respect, the heaviest bean (60 cgms) had no better genetic potentiality than the lightest one (20 cgms). In other words, selection within the pure line, on the basis of bean weight in this case, resulted in no improvement.

2. **Mass Selection.** In this method, a large number of plants are selected from the field population and the seeds from all the selected plants are composited together. This seed mixture is then used to sow the crop plant directly without any comparison trials that are required in the case of pure line selection. This method differs from the pure line selection in that it retains a larger number of lines rather than individual pure lines. This method is safe and quick and retains greater natural variability which may be lost in the pure line selection. It aims at the elimination of only the inferior and defective types which adversely affect the yield and other qualities of the original variety and retains all that is best in it.

3. **Hybridisation and Selection.** Quite often none of the strains of a self-pollinated crop plant developed by selection possesses all the

desirable traits. The favourable genes are often scattered in two or more different races or strains of the heterogeneous mixture of natural population. Plant breeding in self-pollinated species aims at combining, in a single variety, the desirable genes that are so scattered. This objective is achieved through hybridisation.

The first step is the selection of parents by the method described earlier. One parent is selected for its established productivity and the other parent selected is one that possesses in a marked degree the other desirable traits. The two are then artificially crossed to produce the F_1 hybrid progeny according to the procedure described on page 211 If the parents in a cross are pure lines for the selected traits the F_1 hybrid progeny will be uniform, though heterozygous. The F_1 plants are then allowed to self-pollinate to produce the F_2 generation. The same procedure of selfing is adopted for the production of the F_3 and subsequent generations. In each generation from the F_2 onward genetic segregation will take place and heterozygosity will be reduced by one-half with each selfed generation and homozygosity will correspondingly increase. For selection of the desirable genotype in the segregating progeny two procedures are commonly employed. These are known as the **pedigree method** and the **bulk method.**

(*a*) **Pedigree method.** This is the most commonly used method. Selection of desirable types is started for superior traits in the F_2 generation and is continued in every succeeding generation produced by selfing, till true-breeding homozygous types or families, each with uniform traits, are developed. This will be achieved by the F_5 or F_6 generation. In this method a record of the ancestory or pedigree is kept for each selection. This record is useful in eliminating selection of closely related individuals whose value is nearly identical.

With the achievement of homozygosity in the fifth or sixth generation selection within a family will no longer be effective, since each family will be a pure line. Selection is now made among the families and those types which possess the desired combination are finally selected. These are then tested to ensure that they breed true for the desired combination and their performance for yield is compared with that of the original bulk. The selected types are then released to the growers.

The pedigree method of breeding is suitable for those crops where the selected characters can be easily seen. It involves much work and record-keeping during the early segregating generations, but it has one great advantage that only a comparatively small

number of superior plants, carrying the desired gene combinations, are required to be used for producing the next generation. Moreover, this method can be used with advantage in crops where individual plants can be harvested separately, as in tobacco, soyabeans, and cotton.

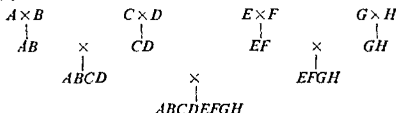
(*b*) **Bulk method of selection.** In this method, a large F_1 generation is raised from the hybrid seeds and the F_2 seeds or grains are collected in bulk and sown in a large plot to raise a large F_2 generation, consisting of hundreds or even several thousands of plants. This process is repeated for several generations, usually up to the F_5 or F_6 generation. Natural selection is allowed to act during all these generations and may be assisted by artificial selection at any stage by eliminating undesirable and inferior types in the progeny. Single-plant selections are then made in the F_6 to F_8 generations and progenies of selected plants are grown in separate rows. Desirable progenies which still show segregation may be subjected to further single plant selections till true breeding strains are established. Superior lines are then grown in separate rows again for multiplication and evaluation as in the case of pedigree method.

The bulk method of breeding is simple and less laborious during the early segregating generations but it requires the growing of a very large progeny in each of the early generations so that the bulk population may offer a fair chance of yielding the desirable segregates. This method is most suitable for close growing and small grained crops and beans and unsuitable for fruit and most vegetable crops.

Plant breeding by hybridisation in actual practice is a long process requiring great skill and patience in the plant breeder. The most crucial part of the process is the ability to recognise and isolate the desirable plants from the segregating progeny of the hybrid. This involves careful observation, exhaustive testing of all selected plants and their progenies, studying the reaction of selected lines to adverse conditions such as disease, drought or cold ; keeping accurate records ; and finally the breeder must be capable of identifying accurately the potentially superior lines. A careful selection of the parent varieties is also essential so that they possess all the traits that are sought to be combined in the progeny of the cross.

4. **Multiple Crossing.** Sometimes no two strains in the natural population possess all the traits that are sought to be combined in the new variety. This may make it necessary to select a third

parent which is then crossed with the F_1 hybrids of the other two parents. Sometimes four, eight or even more parents may be needed in the production of new varieties of some self-pollinated crops, as in barley. In such cases, multiple crosses are produced by crossing pairs of parents, and then crossing the F_1 hybrids in pairs until all parents enter into a common progeny as schematically outlined below:



The resulting hybrid is then used as the starting point for the selection programme.

This system of multiple crossing provides the quickest method for combining genes from several parents. Several new combinations spring up in the F_2 and succeeding generations and production of very large progenies in these generations is necessary to obtain the maximum number of possible genotypes. A handicap with this method lies in the possible production of many undesirable combinations. For obtaining desirable combinations it would be necessary to practise selection in each generation before raising the next. This would be a very long process.

5. **The Backcross Method.** This is a form of recurrent crossing by which some superior genes are transferred to an otherwise good variety but which is deficient in one or more valuable traits. Sometimes an adapted and commercially productive variety lacks in some useful character *e g.*, frost hardiness or disease resistance which is possessed by some other variety. It is then intended to add the good gene or genes of the latter to the former variety. This is achieved by the backcross method. The method is very simple and its technique may be explained by an example.

Suppose a variety *A* is a high yielder but frost susceptible and the variety *B* is frost hardy but poor yielder. It is desired to transfer the hardiness of *B* to *A* without adversely affecting the good qualities of the latter. Two plants from these varieties are selected and crossed to produce the F_1 hybrid progeny. The F_1 hybrid is then backcrossed several times to the parent variety *A* (commercially productive variety). After each backcross selection is made for the desired character of *B*, in this case frost hardiness. The selected plant

is again backcrossed to *A* and selection is again made as before. The commercial parent *A*, to which the superior trait is being added enters into each backcross and is called the recipient or recurrent parent. *B* is the donor parent for the superior character. It does not enter into the backcross and is called the **non-recurrent parent.** This operation of backcrossing to *A* and selection is repeated till a type is obtained which combines the high yielding quality of *A* and the frost hardiness of *B*. This kind of introduction of some genes of one species (in this case *B*) into the genotype of another species (in this case *A*) by hybridisation is called **introgressive hybridisation.** The final selection is self-fertilised till plants that are homozygous for frost hardiness are obtained. A homozygous form selected by this method may be crossed with another similarly selected homozygous form to obtain hybrid vigour.

The backcross maintains the genotype of the recurrent parent and simultaneously a gene (or genes) for the superior trait from the non-recurrent parent is added. Selection is made only for the superior trait contributed by the non-recurrent parent.

6. **Multilineal crosses.** Dr. Borlaugh, Director International Wheat Improvement Project, Mexico, developed a new technique of producing multineal varieties of wheat. A high yielding wheat variety is crossed with a great many varieties, each having a different rust-resistance. Each of these separate crosses in back crossed with the original variety. From these backcrosses selections are then made for both rust-resistance and high yield. Finally, 12 to 16 selections are made. These are then grown in the same field for the final selection of those that show the greatest resistance to rust.

Borlaugh also evolved day-neutral wheat varieties which could be grown in wider areas. It was he who transferred dwarfness and light-insensitiveness to the Mexican varieties. These qualities were responsible for the spectacular success of the Mexican varieties introduced in India.

BREEDING OF CROSS-POLLINATED CROPS

Most of the wild plants and many of our cultivated plants are cross-fertilised in nature. The economic plants in this category include cereals (maize and rye), forage crops (white and red clover), many vegetables and fruits (cabbage, cauliflower, carrots, onion, radish, spinach, pumpkin, water melon, musk melon, raspberry, strawberry, pear, apple, banana, date, fig, grapes, mango, almond,

chestnut, walnut, pistachio), and plants cultivated for fibres and essential oils.

The cross-pollinated plants are heterozygous for many characters and exhibit genetic variability of a high order. The field population of such plants is a mixture of numerous genetically different heterozygous types. Many of these carry deleterious recessive genes concealed in the heterozygotes. Heterozygosity is one of their essential features and is responsible for their adaptedness and productivity. When these plants are reduced to homozygous condition by interbreeding, many types which are homozygous for deleterious recessive genes appear and the result is a diminution of their vigour and productivity. Sometimes, this reduction in plant vigour is very drastic. It is, therefore, necessary that in a breeding procedure the heterozygosity should be either maintained or restored as a final step.

The methods of cross-pollination and the breeding behaviour of cross-pollinated plants are so diverse that the methods used for their breeding cannot be so sharply defined as in the case of self-pollinating plants. The principal methods used for the development of new varieties of cross-pollinated crops, apart from introductions, are (1) selection, (2) hybridisation and (3) production of synthetic or composite varieties.

1. **Selection.** The oldest method of selection used for the development of varieties of cross pollinated crops is **mass selection.** The single plant selection is not practised for the simple reason that these plants do not breed true on account of segregation and it leads to reduction of heterozygosity which is necessary for the vigour of cross-pollinated plants. Besides mass selection, the methods of **progeny selection** and **recurrent selection** are also used.

(*a*) **Mass selection.** The procedure is the same as described for *self-pollinated plants. The seed is collected* from a large number of field plants, which show vigorous growth and desirable traits, and is bulked together. This seed mixture is used to raise the next generation. Mass selection may be repeated in the next generation or may be continued for several generations. After one or several cycles of mass selection, the seed of a number of superior plants is composited and is planted in a separate plot where it is allowed to pollinate at random. The seed mixture from this plot is then released as a new variety.

No progeny tests are made. Selection is based on phenotype and its effectiveness depends upon the extent to which the phenotype is

an expression of the genotype. If the selected phenotype is the expression of good genotype and not that of the environment then this method ensures a great diversity of superior genotypes within the population. This method has, therefore, been successful in the selection and accumulation of those genes which can be identified from the phenotype, for example height of plant, size of ear, protein and oil content, and similar traits. It has not been so effective in improving characters like yield, which is influenced greatly by the environment and which cannot be identified from the phenotype.

This method is simple and easy and gives quick results, but it has several limitations. Firstly, the selection is based on the maternal parent and there is no control over the pollen parent (the selected plants being pollinated by both superior and inferior pollen plants) or the genes that it may contribute to the progeny ; secondly, it is not possible to determine accurately whether the superior phenotype stems from superior genotype or is due to environment. In spite of these limitations mass selection has been successfully used in developing many important varieties of maize, cotton, sugar beets, vegetables and forage crops. Another disadvantage of mass selection results from the reduction in population size which follows. This leads to inbreeding depression. On account of these limitations modified methods known as progeny selection and recurrent selection have been adopted.

(*b*) **Progeny selection and line breeding.** In this method the progenies of selected plants are grown in individual plots in order to determine the breeding behaviour of selected plants In this way it is possible to determine whether the superiority of any selected phenotype is gene-controlled or environmentally induced. Plants whose progeny show better performance are then composited to produce the next generation. Progeny selection is thus very effective in identifying superior genotypes. Progeny selection is practicable only with those crops which are harvested as separate plants and is difficult with small-grained crops like grasses and legumes, which grow in dense stands and are hard to harvest separately.

In the breeding of cotton and sugar beets the following procedure is adopted. Many plants with superior phenotypes are subjected to progeny selection. Plants characterised by the better performance of their progeny are then selected and grown in an isolated plot. Here they are allowed to mate at random, so that all sorts of combinations of genes take place in the seeds. The seed harvested from this plot is then composited and released to the farmer as a new variety. This

procedure is called **line breeding**. To avoid excessive inbreeding, and the loss of vigour that it entails, it is necessary to use an adequate number of lines in making the composite seed and also to take care that the lines are not closely related.

(*c*) **Recurrent selection.** In this method plants that are superior for the desired character are selected and selfed. The seed from these selfed plants is used to grow plant-to-row progenies. From these progenies superior plants are selected and intercrossed in all possible combinations. Hybrid seeds from these crosses are composited to produce population for selection (first recurrent cycle). From this bulk population superior plants for the desired character are again selected and used to grow new plant-to-row progenies. These are crossed in all possible combinations as before and the hybrid seed is composited to grow a bulk population which is the starting point for the second recurrent cycle. The process may be continued as long as improvement in the character under selection continues. This is called recurrent selection by which is meant reselection generation after generation, with interbreeding of selected plants to provide for genetic recombinations.

Recurrent selection helps to concentrate the most favourable genes for a particular desirable character in the original heterozygous population without a marked loss of genetic variability. It differs from mass selection in that in this the gene contribution of the male parent is also controlled.

The procedure described above is used when selection is practised for quantitative characters which can be easily identified by the phenotype, for example oil and protein content in maize, fibre strength in cotton, and sugar content in sugar beets. Where an accurate judgement of the genotype cannot be made from the phenotype, as is the case with yield, the progeny test method is adopted to choose the genotypes which are to be used as parents for the next generation in recurrent selection.

2. **Hybridisation.** Hybrid plants are known for their vigour, growth, size and yield. The utilisation of hybrid vigour was first applied to the development of maize varieties. It has now also been applied to the breeding of hybrid varieties of bajra, jowar, sugar beets, onions, tomato, grasses and vegetable crops.

As applied to maize, the procedure in the development of hybrid varieties involves three steps : (1) selection of desirable plants in the open pollinated population, (2) selfing these plants through several generations to produce uniform homozygous inbred lines, and (3)

ed in an increase of 15 bushles per acre giving an aggregate increase of about 900 million bushles per year.

Double cross hybrid varieties of maize have also been developed in India, especially at the I.A.R.I. and the Punjab Agricultural University, Ludhiana. Some of the well-known hybrid varieties are Ganga 101, Ganga 2, Ganga 3, Ganga 5, Ranjit, Deccan, EH 238, EH 461 and EH 450. Only in May 1967 the I.A.R.I. released to the farmers a new hybrid maize variety "Jawahar'. Hybrid varieties of Bajra (HB1), Jowar (CSH1) and fodder grasses have also been produced at the I.A.R.I. and at the Punjab Agriculture University, Ludhiana. These excel the local open pollinated varieties in yield.

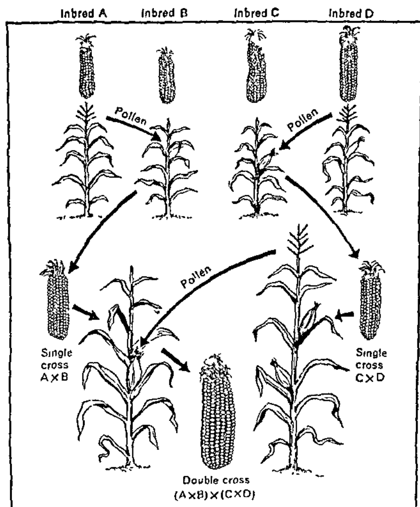


Fig 12 1. Method of producing double cross hybrid maize

It has been observed that greater diversity *in the inbred lines* used in hybridisation leads to greater *heterotic effect on the yield of* the hybrid varieties. It is, therefore, desirable that a large number of inbred lines be used in crosses

In breeding procedures it is necessary to determine the combinability (productivity in crosses) of the inbreds. *Previously, this was* done by crossing individual inbreds with as many other inbreds as possible. A very large number of tests was necessary. The number of crosses that would have to be made is represented by the formula $n(n-1)/2$ where n is the number of inbred lines. Thus, with 25 inbred lines 300 crosses would have to be made. *This method has now been replaced* by what is known as the 'top cross' procedure. Each inbred line is crossed with the original variety. The inbreds which perform well in such *top* crosses also give high yielding single crosses. Those inbreds whose top-cross hybrids are low yielders are rejected. The remaining inbred lines are *then* crossed with one another and the hybrids tested for yield. The number of trials under this method is equal to n. The number of promising inbreds and the number of crosses to be made among the inbred lines is thus greatly reduced.

3. Synthetic or Composite Varieties. A synthetic variety is one which has been synthesised from all possible *intercrosses* among a number of *selected* genotypes. Only plants or strains with superior hybrid combinations are put into the synthetic variety. A synthetic variety differs from a variety produced by mass selection in that in mass selection the composite seed is obtained from phenotypically superior plants which have not been subjected to progeny tests nor tested for the performance of the hybrid combination. In synthetic varieties only those plants are used which have been tested for superior genotypes and for their ability to produce superior progeny when crossed in all combinations. Moreover, in mass selection there is no control over the male parent while in the production of synthetic varieties pollination is controlled. Several synthetic or composite varieties of maize have been produced in India and those released in 1967 are Jawahar, Ambar, Vijay, Vikram, Kissan and Sona. An advantage of the synthetic varieties is that seed obtained from the crop, if grown away from local varieties, could be used again for raising the next year's crop whereas in the case of hybrid varieties a farmer has to buy fresh seed every year. The yield potential of synthetic varieties is as high as, and often greater than, that of hybrid varieties.

BREEDING OF VEGETATIVELY PROPAGATED PLANTS

Some field crops and many garden and fruit plants are normally propagated asexually by means of corms, bulbs, rhizomes, stolons, tubers, etc. or by the horticultural methods of cuttings, budding and grafting. To this category belong the sugarcane, potatoes, sweet potatoes and many grasses, apple, pears, plum and many other fruit trees, grapes, pineapples and many ornamental shrubs and trees. The vegetatively propagated plants are highly heterozygous and in sexual reproduction do not breed true due to segregation. They, however, breed true to type in asexual reproduction, because in this method reproduction takes place by the continuation of the mitotic process of growth. The natural population of vegetatively propagated plants is not only heterozygous but is also a heterogeneous mixture of several types. Each type is known as a **clone**. A clone is a group of plants which is propagated vegetatively from a single plant. All the plants in a clone have identical genotype and bear the same characteristics as the original parent plant unless mutations occur. The asexual method of reproduction is of unique significance to the plant breeder in as much as it provides an easy and rapid method for producing a large number of genetically identical indivduals irrespective of the degree of heterozygosity of the genotype. Two procedures are available for the breeding of asexually propagated plants. These are (1) clonal selection, and (2) hybridisation.

1. Clonal Selection. The natural population of asexually propagated plants is usually a mixture of several clones. All plants within a clone have a remarkably uniform phenotype because of their identical genotype. Selection consists in picking out the superior clone from the population. The genotype of the selected clone is then perpetuated by asexual propagation. This procedure only isolates what is best in the existing population but in no way improves the characteristics of a variety.

2. Hybridisation. Sexual reproduction is resorted to when improvement in the genotype of the asexually propagated plants is sought. This brings about recombination of genes as a result of segregation. Plants of superior clones are crossed to produce the F_1 hybrids. Since the parent clones are heterozygous, segregation will occur in the F_1 generation. Each F_1 plant is thus a potential source for a new clone. Selfing to produce an F_2 generation is seldom practised as it may have an adverse effect upon vigour. Superior plants from the F_1 progenies are picked out and propagated vegeta-

tively to establish a new clone. The clone is then tested for yield and other desirable traits.

Sometimes wide crosses are made to introduce special traits, such as disease resistance, from related wild species. This may also bring in some undesirable genes from the wild parent. Elimination of such genes is achieved through repeated backcrosses to the cultivated species which acts as the recurrent parent. Since backcrossing is a form of inbreeding, this procedure may result in reduction of vigour. This may be avoided by using two or three cultivated varieties as recurrent parents. The backcrosses are then made successively to one and then to another of the cultivated varieties.

ROLE OF MUTATION IN PLANT BREEDING*

Mutations of various kinds—gene mutations, chromosomal mutations and genomatic changes—have been described in some details in chapter 10. Besides providing the raw material for evolution, mutations also provide the material for recombination and selection for plant breeding. There can be no selection without variation. While there is a large fund of variation occurring in natural population, it is not inexhaustible, at least, on *theoretical grounds. Recombinations produced by hybridisation* also provide an enormously large source of variation to the plant breeder. Mutation and related phenomena (like polyploidy) are an inexhaustible source of new variations. They are, in fact, the ultimate source of all variations, whether for *evolution of new* species or for the breeding of new varieties. A part of the mutational variations may not be necessarily useful to the plant in natural selection. Quite often, breeder's selection and natural selection operate *in opposite directions.* The plant breeder must always *be on the* lookout for any useful mutation that may naturally spring up *in his* population. Thus, when a severe epidemic of some plant disease breaks out, some plants may not be affected by the disease. There is quite a fair probability that the resistance of these plants was due to mutation. Mutations are more frequent *in cross-fertilised* than in self-fertilised plants. The success of a plant breeder depends in a very large measure on his ability to detect the small mutations and select the right one. If necessary, *the desirable*

*This section should be read in conjunction with the sections on gene mutations and chromosomal mutations given in the chapter 10. Students are advised to read those sections carefully before reading this section

mutation may be incorporated in the existing varieties by hybridisation. Great improvements sometimes occur in crop and garden and fruit plants by spontaneous mutations occurring in nature. Only in 1968 a new mutant strain of banana was produced by Pericherla Bhaskara Raju, a horticulturist of West Godavari district, in Andhra Pradesh. Raju discovered the new strain in a sapling in his farm by accident. He isolated the sapling and reared it with special care. It yielded a bunch of 150 bananas, each about 14 inches long and 2-5 inch in diameter and weighing between 300 and 400 gms. This 'wonder Bhaskara banana' is golden coloured and is more delicious than the ordinary table variety. But for Raju's observant eye, the mutation might have been lost.

The giant variety of gram (*Cicer gigas*), and of groundnut (*Arachis hypogea*, var. gigantea) are examples of improved forms arising through mutattion. The improved strain of paddy G.E.B. 24 and that of ragi E. C. 3735 arose in this manner. A spontaneous mutation in tobacco turned out to be of great commercial value. All the wild relatives of tobacco produce an enzyme which converts nicotine into nornicotine. A mutant which suppresses the action of this converter enzyme has been picked up by man and stabilised in our present day varieties Similarly, the lint hairs in cotton is the result of mutation produced in the wild relatives of cotton which do not possess the lint hairs so essential for making cloth. Irradiation is a potent tool in the hands of geneticists and plant breeders and can bring about the transmutation of species in one big jump.

Mutation and selection are weapons of great service to the plant breeder. With their help he can change the genotype and phenotype of plants according to his needs. All plant breeding programmes now include the production of artificial mutations in crop plants with the help of such mutagenic agents as atomic radiations of various types. These include X-rays, ultraviolet rays, neutrons and radiations from radioactive isotopes. High energy radioactive radiations are applied in order to alter hereditary properties of plants and sometimes undesirable traits are changed by mutation into desirable ones, as happened in the case of Sharbati Sonora wheat described below.

Mutations thus induced have been responsible for some of the improved varieties of crop plants. The beneficial results are an increased crop production, early and late varieties and varieties resistant to disease, frost or drought. Very useful work in this

direction is being done at the Indian Agricultural Research Institute, New Delhi, where more than 1,000 mutations of wheat and barley have been produced with the help of atomic energy. A few examples will serve as illustrations. The imported Mexican wheat Sonora 64 was red in colour. Out of the induced mutations produced by gamma irradiation was evolved the Sharbati Sonora variety, with amber coloured grains. This new variety yields a harvest of 7,000 lb. per acre. Improved awnless wheat, when irradiated with X-rays and gamma rays, produced an awned variety (Swaminathan 1965). The mutation was useful as it protected the grains from birds Awns contain chlorophyll and increase seed weight by photosynthesis. This gives higher grain yield especially in dry areas.

Several new sub-species of bread wheat, (*Triticum aestivum*) and emmer wheat series, to which macroni wheat *T. durum* belongs, have been developed by this method. Thus, a new bread wheat variety N. 797 was obtained by treatment with radioactive sulphur and selection. The mutant was a jowar-like wheat in which a single stem bears an earhead of 13 to 14 branches (Plate 1). This new variety was dwarf and produced twice as many grains per ear as the parent variety.

Twenty new varieties of barley have been produced from N.P. 104 through irradiation. Some of them are expected to increase the crop yield by 25 per cent.

More examples of new strains and improved varieties of crop plants produced through atomic radiations are given below :

Wheat —Increased resistance to stem rust
—Improved baking quality, superior glutenin content
—Increased straw strength

Oats —Resistance to crown rust and stem rust
—Higher yield combined with late maturity
—Increased straw strength

Barley —Mildew resistance
— Increased malt quality due to higher diastatic content
—Increased yield due to higher kernel weight or increased tillering
—Increased straw strength

Flax —Superior fibre content
—Increased straw yield

White mustard --Increased yield of seed and oil

Mutations also occur naturally in vegetative tissues of plants. These somatic mutations occur commonly in the buds and may be of the nature of gene mutations, chromosomal alterations or genomatic changes produced by somatic doubling. They can also be induced artificially. These are of no avail in sexually reproducing plants but in plants, that are propagated vegetatively, selection from somatic mutations leads to improvements, as in ornamental plants like chrysanthemums and dahlias, crop plants like sugar-cane and potato, and in fruit plants. Somatic mutations in Cayenne pineapple in Hawaii Islands gave rise to three new strains.

A famous example of such (bud) mutation is the navel (seedless) orange. It was discovered on two orange trees in South America in the nineteenth century. Buds from these trees were grafted on trees that produced oranges with seeds. Eventually, many seedless orange groves were developed and all have their ancestry rooted in the two trees that produced the original mutation. Dawn grape-fruit also arose as a bud mutation. Similarly, in potato many well-known varieties like Russet Burbank, Cobbler, Red Triumph, Red Pontiac, and others arose in this way.

ROLE OF POLYPLOIDY IN PLANT BREEDING

Different forms of polyploidy have been described in chapter 10. The relevant section in that chapter should be reread thoroughly before proceeding with this section. Besides its role in evolution, polyploidy has played an important role in the production of many of our economic plants. Many of our important crop plants like wheat, oat, sugar-cane, flax, cotton, potatoes and tobacco, as also many grasses and forage plants, and many fruits and vegetables are natural polyploids of various degrees. Common examples of autopolyploid cultivated plants are potato, sweet-potato, alfalfa, banana, peanut (groundnut) and coffee. Allopolyploid cultivated plants include wheat, oats, sugar-cane, cotton, tobacco and plums.

The wild and cultivated wheats form a series of diploid (2N=14 ; *AA*), tetraploid (4N=28 ; *AABB*) and hexaploid (6N=42 ; *AABBDD*) types with the basic number 7. The bread wheats belong to the hexaploid group. The tetraploid Emmer wheats (*AABB*) contain two distinct genomes (*A* and *B*) and the present evidence suggests that these originated from amphidiploids between *Triticum*

monococcum (*AA*) and *Aegilops speltoides* (*BB*). The present-day hexaploid wheats arose as a result of hybridisation between the tetraploid wheats of the Emmer group (*AABB*) and a diploid type (*DD*), followed by chromosome doubling in the hybrid. The diploid

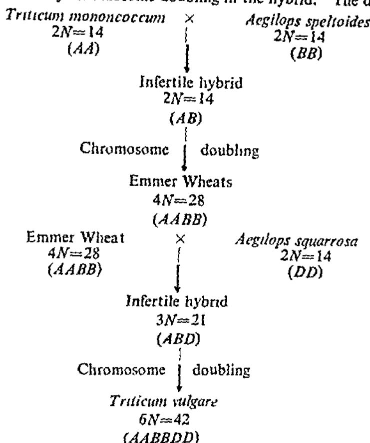


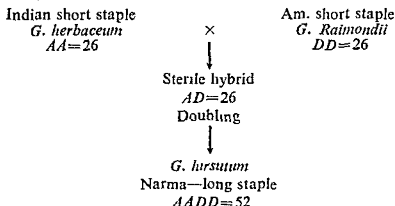
Fig. 12.2. Origin of *Triticum vulgare* by interspecific hybridisation and polyploidy

parent of the common wheats appears to be the goat grass, *Aegilops squarrosa* (2N=14). The origin of bread wheat, *Triticum vulgare*, (syn. *T. aestivum*) ($2N$=42 or $6N$=42) is illustrated in figure 12.2.

A synthetic hexaploid wheat has been produced by crossing the goat grass with Emmer wheats and doubling the chromosome number in the hybrid. The synthetic wheat resembles the common bread wheat and crosses freely with it, producing fertile hybrids.

Cotton and mustards provide other examples of the role of polyploidy in the production of crop plants. The American cultivated cottons have the chromosome number 2N=52 and the Asiatic cottons and wild American species of cottons have 2N=26. It has

been shown that the American cultivated cottons are allotetraploid (amphidiploid) forms of the other two forms and were produced as a result of crossing between them, followed by chromosome doubling in the hybrid. Harland and Beasley succeeded independently in producing a synthetic American cotton (2N=52). They intercrossed *Gossypium thurberi*, a wild American species (2N=26), and *G. arboreum* (2N=26), an Asiatic cotton, and then doubled the chromosome number of the F_1 hybrid by the colchicine technique. The synthetic species (now 2N=52) resembled the American cotton and crossed freely with the latter, producing fertile hybrids. The famous long staple Narma cotton (*G. hirsutum*) is an allopolyploid obtained by crossing Indian species *G. herbaceum* with the American diploid species *G. Raimondii* as shown below :



A similar situation obtains in the mustards. By following the technique outlined above it has been shown that *Brassica juncea* (brown mustard, 2N=36) is an allotetraploid between *B. nigra* (black mustard. 2N=16) and *B. campestris* (rape, 2N=20) ; and *B. napus* (turnip, 2N=38) is an allotetraploid between *B. oleracea* (cabbage, kohrabi, 2N=18) and *B. campestris* (2N=20).

Similarly, there is evidence that the common tobacco, *Nicotiana tabacum* (2N=48), is an allotetraploid between *N. sylvestris* (2N=24) and *N. tomentosa* or some allied species (2N=24). *N. tabacum* is known only under cultivation and does not occur as a natural species. Evidence of its tetraploid nature is derived from the fact that the crossing of the two diploid species named above produces a sterile hybrid which on chromosome doubling becomes fertile and resembles the common tobacco in many respects. Evidently, *N. tabacum* arose in this manner. This was probably followed by a long period of evolution, bringing into ex-

Mendelian variation the numerous varieties of common tobacco. This happened in South America long before Columbus, because by the time of discovery of America *N. tabacum* was a highly developed species. A new hexaploid species of tobacco, *N. digluta* (2N=72) has been artificially synthesised by crossing the diploid species *N. glutinosa* with the tetraploid *N. tabacum* and doubling the chromosomes of the F_1 hybrid.

The artificial induction of chromosome doubling by the colchicine technique has opened up new fields for the production of polyploid plants. More successful results are obtained in cross-fertilised plants and those that have fewer chromosomes than in self-fertilised plants and those in which the chromosome number is high. Superior agronomic autopolyploids have been obtained in sugar beet, turnip, mustard, rye and red clover whereas those produced in rape, flax, soyabeans and potatoes turned out to be of poor agronomic value.

One difficulty encountered in seed crops is the relatively lower fertility of the autopolyploids. This results in fewer seeds per plant. Here selection for higher fertility in segregating generations is desirable and is likely to lead to greater seed-setting types. Most of our crop plants are highly perfected forms which through natural selection have come to develop perfect epharmony with the conditions of their environment. Many of them are already polyploids of different types and degrees and further increase in their chromosome number is not attended with any improvement.

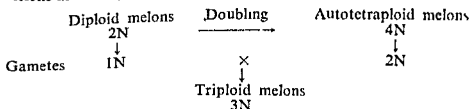
Allopolyploidy is more important than autopolyploidy in crop plants. Allopolyploidy restores fertility to sterile interspecific crosses and makes possible hybridisation between species that do not cross in nature as is illustrated by the case of American and Asiatic cottons described above. In this way, genes from one species may be transferred to the other species. Thus, genes for resistance to the downy mildew contained in the Australian species of *Nicotiana* were transferred to the economic but susceptible *N. tabacum* by hybridisation and induction of polyploidy in the F_1 hybrid. *N tabacum* contains the alkaloid nicotine. Another alkaloid anabasine which is more active than nicotine is contained in the Australian species *N. glauca*. Allotetraploid of these species is richer in anabasine.

On account of the larger number of genes, polyploids possess a greater potential for variability arising from mutation. Structural changes in the chromosomes are also likely to be more frequent and

more diverse in polyploids than in diploids and a greater variability is likely to result from crossing with different species. Moreover, hybrid vigour not only persists in the polyploids but is also of a higher order than in the diploid plants.

Tetraploid (autotype) grapes produced in somatic tissues after pruning or near injured tissues are now cultivated in the U.S.A., Japan and England. Although the number of berries in a cluster was low in the tetraploid, yet these far exceeded in size and weight those produced on the diploid prototype and contained fewer seeds per berry.

Triploids are usually sterile but in some cases they are fertile. A triploid tea and a triploid mulberry are popular in Japan on account of their resistance to cold. In vegetatively propagated fruits, sterility of the triploid is of advantage as the fruits tend to be seedless. Many varieties of apples grown in America and bananas are triploids. In plants that are grown for their vegetative parts, such as roots and tubers, triploid sterility is not a serious problem. Triploid beets excel the diploid forms in size of root and sugar percentage, and are now grown commercially. Seedless large triploid water melons are widely cutivated in Japan and are superior to the diploid



and tetraploid forms in yield and are resistant to the wilt disease which is highly destructive to the diploid varieties. Due to the inability of the triploid plants to set sufficient triploid seeds, seeds for the cultivation of triploid varieties are obtained by crossing diploid and tetraploid plants, the latter being used as the female parent. The reciprocal cross is unsuccessful.

Karpechenko (1926) synthesised an intergeneric allopolyploid *Raphano-brassica* by crossing radish and brassica followed by chromosome doubling with the help of colchicine. Unfortunately, the polyploid combined only the uneconomic characters of the progenitors. The first example of man-made synthetic crop with possibility of commercially valuable characters is *Triticale* (ryewheat) produced by Muntzing by crossing *Secale cereale* (rye) and *Triticum vulgare* (wheat) and subsequent chromosome doubling in the hyb

Secale cereale × *Tr. vulgare*

↓ Chromosome doubling

Triticale

Further breeding of *Triticale* and selection by Borlaugh in Mexico and at the IARI, Delhi have resulted in forms that are promising from an agronomic point of view. The Russian scientist Pissorev developed day natural and semidwarf varieties of this new species. A new variety of this rye-wheat hybrid, suitable for cultivation in the Rajasthan desert area, has been evolved at the IARI, N-Delhi. The new cereal is more drought resistant than wheat or barley and resembles wheat in productivity and grain characters and in resistance to disease it is like rye. Its ears are larger than those of wheat and they bear bigger and more numerous grains than wheat. It is also rich in protein but its gluten content is low, with the result that it does not make good *chapatis* and bread. Another intergeneric allotetraploid is *Aegilotriticum* obtained from a cross between *Aegilops sp.* and *Triticum sp.* Borlaugh is exploring the possibilities of hybridising wheat cells and rice cells at the cellular level to produce what he calls "whrice", a combination of wheat and rice.

Earlier in this section was described the artificial production of certain naturally occurring species of *Brassica*. Recently, new synthetic allopolyploids of secondary type with potentialities of agronomic values have been produced. These include *B. napojuncea* (N=37) from a *B. napus* (N=19) × *B. juncea* (N=18) cross; *B. oleracea napus* (N=28) from *B. oleracea* (N=9) × *B. napus* (N=19) cross; *B. juncea-campestris* (N=28) from *B. campestris* (N=10) × *B. juncea* (N=18) cross; *B. napo-campestris* (N=29) from *B. napus* (N=19) × *B. campestris* (N=10) cross.

BREEDING FOR DISEASE RESISTANCE

disease the entire crop may be lost as happened in the potato famine in Europe in the middle of the last century. In terms of money the annual loss in India on account of plant diseases runs into several hundred crores of rupees. In the U.S A., it has been estimated that plant diseases caused by micro-organisms are responsible for an annual loss of about 3 billion dollars and the loss caused by insect pests exceeds this figure by about a billion dollars. These are huge figures and mean a good deal both to the cultivator and the nation. It is, therefore, no wonder that in all agricultural schemes great importance is now attached to the production of disease-resistant varieties. A disease does not affect all plants equally. Casual examination of a wheat field, for example, in the month of February or March will show that while some plants are more severely infected with the rust disease, others are affected only in a mild way and there will be some plants that are entirely free from the disease. The severity of the disease on the plants of the first category is due to their susceptibility to the disease. The mildly affected plants are relatively resistant to the disease and the plants of the last category are said to be immune to the disease. In a general way, cultivated plants are susceptible to diseases and the wild plants are disease-resistant in varying degrees. The reason for this is that in earlier days selection of cultivated plants was made for such economic characters as yield, quality etc., and no attention was paid to disease resistance. In the case of wild plants, however, natural selection would always operate in favour of resistant forms.

Disease resistance is a hereditary character. In most cases it is dominant and in some cases it may be recessive. In some plants resistance is due to a single gene and in others it is the result of interaction of several genes.

The first principle in breeding for disease resistance is selection. Whenever a disease appears in virulent form there will be some plants in the population of the attacked species that are resistant to the disease, otherwise, survival is out of question. Their resistance must be due to intrinsic quality which springs from the genotype. Natural selection thus operates towards the preservation of the resistant types. Artificial single-plant selection of such resistant forms as are met with in natural populations and using them as stock for raising future generations can perpetuate their resistance genes. Besides the genes for resistance that already exist among plant species, new mutations imparting disease resistance provide additional material to the plant breeder.

Disease resistance is not the only character that is desired in plants. Economic characters such as yield and quality are important. In cultivated plants a combination of disease resistance and economic characters is the ideal that is sought to be attained. As already stated, the good traits are scattered in the population. The wild plants show a greater resistance to disease than the cultivated plants. When the wild plants were brought under cultivation, man's interference with nature resulted in the loss of disease resistance which the wild plants possessed. The reason is that in cultivated plants the pressure of artificial selection operated in favour of such traits as yield and quality and the trait of disease resistance was ignored. It is now desired to bring about a combination of economic traits with disease resistance. The method for achieving this objective is hybridisation and selection.

As cultivated varieties of plants mostly lack disease resistance, the first step in all breeding programmes is the search for resistance genes. For this it is necessary to survey the closely related forms in all parts of the world. The best centres of disease resistance are likely to be found in the primary centres of origin of the crop plant or those secondary centres where the crop has been under cultivation over a long period. Natural mutations and those induced artificially also provide another source of disease resistance. By repeated selections, pick out those forms that show the highest degree of resistance. A crop is often susceptible to several diseases. By selection and hybridisation resistance to as many diseases as possible is first concentrated in a single variety. In the case of wheat, for example, resistance to all the three rusts and smut disease is sought to be combined in one strain. This is a huge task and involves hundreds of crosses and back-crosses till a strain that is homozygous for multiple resistance has been produced. The disease resistant wild plants are usually inferior in agronomic characters. The next step, then, is to transfer this combination of disease resistance to the economic varieties by the hybridisation technique explained earlier in this chapter. This work is by no means an easy one. Quite often, it involves multiple crosses and back-crosses to bring about a combination of resistance and agronomic characters. Selections for resistance are made from the F_2 generations onwards till homozygous forms are obtained.

Sometimes, close linkage of resistance with uneconomic characters, and failure to form fertile hybrids set limits to the achievement of hybridisation. The first difficulty is overcome by inducing chro-

mosomal breakage by irradiation and looking for the desired recombinations. In the second case the technique of induced allopolyploidy is resorted to.

Where disease resistance in a closely related form is controlled by a single major gene, the problem of combining it with economic characters is not a difficult one. In such cases a desired recombination can be effected by natural or induced chromosomal rearrangements coupled with back-crossing to the economically valuable varieties. Wherever, however, disease resistance is due to the interaction of several genes, the recovery of a synthetic form which combines disease resistance and the complex economic qualities is a difficult proposition, because of the close linkage of disease resistance with inferior qualities.

Breeding for resistant varieties of economic plants is a continuous work, requiring great patience and persistence. One of the reasons is that mutations in the pathogenic organisms may result in the production of more virulent forms and the resistance of the plant may break down. Forms adapted to the mutant pathogen have then to be searched for. Again, there is always the hope that continuous effort in the direction of breeding may lead at some time in the future to a more efficient and stable combination of high level resistance and more valuable economic characters. New sources of disease resistance may come to notice and it may be possible to bring together resistance to a larger number of diseases.

In spite of the many handicaps inherent in work of this nature, efforts in this direction have been rewarded with considerable success but much yet remains to be achieved. In the case of wheat, for example, the ideal of the breeder is to develop agronomic varieties which combine resistance to the several races of the three forms of rust and also the smut disease, with high yield and good milling and baking properties. Intensive work is being done in India and other countries especially in the U.S.A. towards the realisation of this ideal. The work is very much complicated due to specialisation of parasitism in species of *Puccinia*. Disease resistance occurs more widely in the Emmer group of wheat ($2N=28$) than in the economically valuable Vulgare groups ($2N=42$). By hybridisation between members of these two groups and selection were produced the rust resistant economic varieties Hope and H44. The popular American variety, 'Thatcher, was the result of a double cross (Marquis × Ilumillia) × (Hanred × Marquis). This commercial variety is famous for its yielding capacity. Rust resistance was introduced into it

by crossing it with the variety Hope. Similarly, a variety that combines resistance to rust and bunt diseases has been produced in the U.S.A. from a cross between bunt resistant White federation and the rust resistant Hope.

Rust resistant varieties of wheat have been produced in India also. Some of these have been mentioned earlier. NP 809 is resistant to yellow, orange and black rust and has been found to give good results in the hilly regions of Punjab, Himachal Pradesh and Uttar Pradesh. Another highly rust resistant variety is NP 770 obtained from the cross NP 4×Konoso, a resistant Japanese variety. PV 18 developed in the Punjab and Chhoti Lerma (S 331), evolved at the U.P. Agricultural University, are highly resistant to all the three rusts ; PV18 is also resistant to loose smut and is a high yielder. WG 139, WG 76, WG 175, and C 307 have been found to be highly resistant to the rusts and loose smut in the hilly areas. Breeding work by Indian geneticists has also produced promising results in other crop plants. Some of these are mentioned below.

1. **Sugarcane.** This crop is subject to a number of diseases, namely, red rot, root rot, mosaic, wilt and smut. Very commendable work has been and is being done at the Coimbatore Research Institute and the resistant varieties produced there are now grown the world over. Quite often, a variety which is resistant to one disease is susceptible to others. Moreover, resistance of a variety to a disease is not universal and may break when the resistant variety is grown in other countries. Selection for resistant varieties has, therefore, to be made according to local conditions and the diseases prevailing in different regions. Examples of varieties resistant to various diseases in India are given below. **Red rot,** Co 356, Co 393, Co 419, Co 421, Co 508, Co 527; **Mosaic,** Co 214, Co 315, Co 356, and P.O.J. 2878; **Wilt,** Co S 254; **Smut,** Co 290, Co 449 and Co 617. Examples of varieties which show resistance in other countries are Co 201 which is resistant to red rot and root rot in the U.S.A., Co 290 resistant to root rot in the U.S.A. (smut resistant in India), and Co 496 and Co 497 resistant to mosaic in the U.S.A.

2. ***Cotton.*** Common diseases of Indian cotton are fusarium wilt, root rot and angular leaf spot or bacterial blight. While *Gossypium arboreum* and *G. herbaceum* are immune to the blight diseases, susceptibility to the other two diseases is a common feature of all the three cultivated Indian species. Breeding work has resulted in the production of varieties Vijay, Jaywant, Jarila, Verum 262 and Verum 436 which are highly resistant to wilt and

L.S.S. which shows partial resistance to root rot.

3. **Rice.** Greatest damage to the crop is caused by the blast disease. As a result of breeding work in South India two highly resistant varieties Co 25 and Co 26 have been obtained by transferring the resistance of inferior variety Co 4 to the highly productive but susceptible Madras variety Korangu samba. A new variety, Kashmir 60 has been evolved in Kashmir from a cross between Chinese paddy and Japanese paddy. The former is blast resistant but a prey to shedding. The Japanese variety is free from shedding but blast susceptible. The hybrid Kashmir 60 is resistant to both shedding and blast disease and also to gales and hail-storms. It is also more prolific and tasty than its parents.

4. **Gram.** G 24 and G 17 have been evolved as resistant to gram wilt in the Punjab. C 1234 has been evolved as a blight resistant cross and is sown in blight affected areas.

13

BREEDING OF SOME CROP PLANTS IN INDIA

VERY extensive work on the breeding of crop plants is being done in India. For a co-ordinated plant breeding programme the Government of India set up an Indian Council of Agricultural Research (I.C.A.R). The principal plant breeding centres are the Indian Agricultural Research Institute, New Delhi, Potato Research Station, Simla, Sugar-cane Breeding Institute, Coimbatore, Punjab Agricultural University, Ludhiana, Uttar Pradesh Agricultural University, Pantnagar and several other Agricultural Universities. Hundreds of scientists are engaged in the gigantic task of increasing agricultural production and achieving self-sufficiency in the country's food requirements. The only solution to the present food crisis lies in the development of improved varieties of food plants, varieties with higher yield potential, varieties resistant to cold, drought, diseases and insect pests, early maturing varieties and varieties that are resistant to lodging so that they can stand the increased application of soil fertilisers.

Plant breeding is a long and continuous process, especially in the case of disease resistant strains. Mutations in the pathogenic organisms make the erstwhile disease resistant strains susceptible to them in various degrees and search then has to be made for new genes resistant to the mutated pathogens.

The work of plant breeders in India has been attended with considerable success. Some of the outstanding commercial varieties of crop plants developed in recent years include wheat varieties Lerma Rojo, C 306, PV 18, Kalyan Sona, WG 139, Sonora 64

HD 64-1406, and NP 818 ; S 530, a high yielding variety of bajra, with self-protective bristled ears against bird damage ; CHS 1 and CHS 2 varieties of hybrid jowar, and C 302 variety of Kalkattia tobacco. The development of hybrid bajra No. 1, the first commercial hybrid developed anywhere in the world and its release by the I.C.A.R. for cultivation throughout the bajra growing states of the country is our most outstanding achievement. This hybrid yields almost 100 per cent more than the standard varieties in the different states.

It must be noted that the evolution of superior varieties is not the be-all and end-all of our agricultural problems. Attention must also be paid to the environmental requirements of our crop plants. A regular and continuous supply of irrigation water must be ensured in rain-fed areas because of uncertain incidence of rain. Greater use must be made of manures and fertilisers to improve the texture and fertility of the soil. India must produce two million tonnes of nitrogen and phosphate fertilisers annually to achieve self-sufficiency in food.

With this we may now proceed to give a brief account of the breeding of some important commercial crops in India. This account is mainly based on the breeding work done at the I.A.R.I., New Delhi, various Research Institutes and Agricultural Universities, especially the Punjab Agricultural University, Ludhiana, and the U.P. Agricultural University, Pantnagar.

WHEAT

In India wheat is the second major cereal crop next only to rice. The most commonly cultivated wheat species in India is the hexaploid wheat *Triticum aestivum* (or *T. vulgare*) belonging to the Vulgare group. The marconi wheat *T. durum* (Emmer group) is also cultivated but to a much less extent.

Improved Varieties. Breeding is done for high yield, size and colour of grain, protein content of grain, resistance to drought, lodging and disease, and *chapati*-making quality. Among the traditional standard varieties for Punjab and Haryana are C 591, C 273, C 281, C 286, C 518, 8-A and 9-D. In 1964 a new high yielding wheat variety C 306 was released to the farmers in the Punjab. It was evolved from a complex cross [(Regent 1974×Chz-3) ×C 591]×(P19×C281), and gave higher yield than the older recommended varieties. It soon became the standard universal variety in Punjab and Haryana, excluding the submontane tract, on account

of its uniformly good performance under all conditions. It can be grown successfully under varying conditions of soil moisture, sowing date and fertility level except the too rich lands where it falls down (lodges). It is suitable for late sowing and for rainfed (barani) areas and significantly outyielded the standard C 281 in Haryana.

Other high yielding Indian wheat varieties are N.P. 4, N.P. 52, N.P. 125, N.P. 165, HD 1925 and Pusa Lerma of the I.A.R.I. Delhi; U P. 215 from Pantnagar, AO 68, AO 90, A 115 and *Sharbati* wheat of Madhya Pradesh, and Bansi 274, Jay, Vijay, Nipha-D 4 and Nipha-D 5439 of Maharashtra.

Within the last few years since 1965 a major breakthrough in the production of superior and high yielding wheats has been achieved as a result of the introduction of four dwarf wheats from Mexico, namely Mayo-64, Sonora-63, Sonora-64 and Lerma Rojo-64 A These were tested, bred, and multiplied at the I.A.R.I, Delhi, Uttar Pradesh Agricultural University, Pantnagar and the Punjab Agricultural University, Ludhiana. Many new varieties suited to our conditions have been evolved at these research centres. The original Indian varieties are tall and susceptible to lodging under high fertility condition of the soil. This reduces the grain yield considerably. The Mexican varieties are dwarf and on that account resistant to lodging and excel in grain yield. The development of high-yielding wheat varieties and their cultivation has brought about the first green revolution in the country. The popular Mexican varieties and the new varieties evolved from them are briefly described below.

Lerma Rojo. A semi-dwarf Mexican wheat with one gene for dwarfness. It gives outstanding yield on well fertilised soil and is resistant to lodging and rust disease but the grain is small and red coloured. It also gave significantly higher yield in the submontane region than the standard Indian variety C 286.

Sonora 64. A medium dwarf Mexican wheat with two genes for dwarfness. It is a short-duration wheat and a very high yielder. It is resistant to lodging but is rust susceptible and does not tiller well. Grains are small and red.

PV 18. An outstanding variety evolved at the Punjab Agricultural University, Ludhiana, by selection from the variable dwarf Mexican variety V18. But for its hard red grain, it is very popular and yields very heavy crop on well fertilised soil. It is highly resistant to lodging and moderately resistant to all the three forms of rust and smut and, therefore, suitable also for the submon-

tane region where it significantly outyielded the standard variety C 286. In the plains its yield was 52 per cent higher than the standard Punjab wheat C 273, 42 per cent higher than C 306 and 10 per cent higher than the best Mexican wheat Lerma Rojo. It is the highest yielder even under late sowing condition and matures in 135 days. The average number of grains per head in PV18 is 75 as compared to 55 in most Indian strains It is as good as the improved Punjab wheats in grain quality and straw but its greatest handicap is the red colour of the grain

The above varieties give a grain yield of 30 to 70 maunds per acre depending upon the soil as compared to 10 to 15 maunds obtained from indigenous wheat. But they suffer from four major handicaps which stand in the way of their popularity. These are : (*i*) red colour of grain ; (*ii*) small size of grain as compared to the indigenous wheat ; (*iii*) grains are more starchy and contain less protein and, therefore, are less nutritious ; and (*iv*) they do not make good *chapatis*, although they are good for preparing bread. Several improved varieties of Mexican wheat, with bold amber grain and good *chapati*-making quality, have now been evolved in India. The more important ones are described below.

Sharbati Sonora. It has been evolved at the I.A.R.I. from the red-grained Sonora 64 by mutation with gamma irradiation. The grain is hard and amber coloured and contains 25 per cent more protein than the parent Mexican variety. It is dwarf and resistant to lodging but slightly susceptible to rusts. It is a high yielder and quick maturing (120 days). Some grains will fall down (shatter) if not harvested a few days before full maturity

Kalyan 227. This is the pride release from Ludhiana and the major achievement of the Punjab Agricultural University for the year 1966-67. A selection from the unselected Mexican dwarf line S 227, its yield is almost as high as that of PV18. It combines the desirable characters of dwarfness (height about 90 cm.), resistance to diseases and lodging, high response to fertilisers and something more—amber colour in grain which has added millions of rupees to its market value. Its grain yield is 32·7 per cent more than that of C 306 and 16·5 per cent more than that of the most popular Mexican variety Lerma Rojo. On account of its amber-coloured grain it is more popular than the red-coloured PV18. It is as good as any indigenous wheat for *chapati*-making. It also gives high yield in the irrigated submontane regions of Punjab and Haryana.

Sona 227. This dwarf variety is also a selection from S 227 and

has been produced at the I.A.R.I. and the U.P. Agricultural University, Pantnagar. This hard amber wheat takes 135 days to mature and is the highest yielder in the country. With this variety a Delhi farmer obtained in 1967 an all-world record of 84·3 quintals per hectare (91·4 mds. per acre). It is moderately resistant to rust and lodging. The wheat breeders at the I.A.R.I. have established that Kalyan 227 and Sona 227 are the same wheat. The integrated variety has been named Kalyan Sona.

Safed Lerma (S 307). This high yielding soft amber-coloured wheat was evolved at the U.P. Agricultural University, Pantnagar. It is slightly higher yielding than Lerma Rojo to which it is similar in other respects. It throws out many stems per seed (tillers well) and is highly resistant to rust diseases but may fall down (lodge) in excessive summer winds.

Sonalika (S 308). Another release from the U.P. Agricultural University, Pantnagar, it is the best and most popular dwarf variety which combines high yield with resistance to lodging and rusts and beautiful grains. The grains are bold, hard and amber-coloured. Its *chapatis* are charmers, its straw yield plentiful and it is highly responsive to heavy doses of fertilisers but subject to heavy losses from shattering (falling down of grain) unless harvested a few days before maturing.

Chhoti Lerma (S 331). This is also a release from the U. P. Agricultural University. It is a high yielding dwarf variety with soft amber coloured grain and is very popular. It matures in 130 days, gives as high yield as S 307 and is highly resistant to lodging and shattering. It is most resistant to rusts and the best insurance against rust epidemics.

It will be clear from the above account that the emphasis now is on the production of dwarf varieties which can stand high doses of soil fertilisers and are resistant to lodging. Our indigenous wheats have no dwarf genes. Semi-dwarf Lerma Rojo has one gene and dwarf Sonora has two dwarf genes. The emphasis now is on the production of wheats with three dwarf genes. Among the 3-gene dwarf varieties evolved at Pantnagar and I.A.R.I., New Delhi are U.P. .01, H.D. 1949 (Moti), Lal Bahadur, E.A. 222-1, H.D. 1941 (Hira), W.L. 202 and W.L. 212 (from Ludhiana). The triple dwarf wheats are shorter than Kalyan sona, bear long ears, give higher yield and do not lodge even under very high doses of fertilisers. Their protein content is high and they compare well with the best available varieties in *chapati*-making quality. UP-301

is a high-protein, amber grain variety and is claimed to be completely rust-resistant and non-lodging.

HD 1949 (Moti) was evolved at the I.A.R.I., New Delhi by selection from a cross between E 5557 and NP 852. The plant is 70-75 cm. high, with many ears which are long, thick and full of grains. The grains are heavy, large, amber-coloured and hard. It matures within 130 days and thus is comparatively safe from black and brown rust.

Hira (HD 1941) from New Delhi is superior to other triple gene dwarf wheats. It is non-lodging even with 130 kg. nitrogen per hectare. Its grain is attractive and rich in protein content. Its crop matures 10 to 12 days earlier than other varieties. It is also resistant to diseases and storage pests. Its yield is 10 to 12 per cent higher than that of Kalyan Sona. It can also be adapted over a wider range compared to other varieties and is recommended for the high-fertility and irrigated areas of Punjab, Haryana, Delhi, Uttar Pradesh, parts of Rajasthan and Madhya Pradesh and also for hilly tracts, including Jammu and Kashmir.

Improved varieties for irrigated submontane regions. The standard variety for this area is C 286. The new Punjab variety PV 18 proved most promising, yielding 5344 kg ha as compared with 2269 kg. of C 286. Kalyan Sona, Lerma Rojo and S-308 also significantly outyielded C 286.

Improved varieties for Hill Areas. In hills, yield is low due to the high incidence of rusts, bunt and loose smut. The present approved variety for these regions is C 253. WG 139, evolved in the Punjab, has been found to be the most promising strain with a yield 58 per cent higher than C 253. New strains evolved at the I.A.R.I., HD 64-1406, NP 818 and HD 64-1339, excelled the best Punjab strains in yield. The near amber coloured wheat Kalyan 227 appears to be very suitable for hill cultivation in Lahul and Spiti at 11,000 ft. It is expected to yield 50 mds. per acre against 10 mds. of the traditional varieties.

BAJRA (*Pennisetum typhoides*)

Bajra (pearl millet) is a cereal food for the poor and also a fodder crop. Its cultivation occupies about 930,000 hectares in the Punjab and Haryana. Till 1964 the approved varieties were A1/3 for irrigated areas and T55 for rainfed (barani) areas. A new variety S530 is fast becoming popular with growers in irrigated areas or

has been produced at the I.A.R.I. and the U.P. Agricultural University, Pantnagar. This hard amber wheat takes 135 days to mature and is the highest yielder in the country. With this variety a Delhi farmer obtained in 1967 an all-world record of 84·3 quintals per hectare (91·4 mds. per acre). It is moderately resistant to rust and lodging. The wheat breeders at the I.A.R.I. have established that Kalyan 227 and Sona 227 are the same wheat. The integrated variety has been named Kalyan Sona.

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K28 gave considerably more yield in the Kulu valley than the earlier varieties KB71 and K24.

MAIZE

The local open pollinated variety yields about 1,500 kg. per hectare. Within the last seven years great increase in the yield of maize has been brought about by the introduction of hybrid varieties. The year 1961 marked the beginning of the era of hybrid maize when two hybrid varieties, Ganga 101 for the plains, and VL54 for the hill areas of the Punjab, were released. Ganga 101 yielded 86 per cent more than the local variety. In 1964 new hybrid varieties, Ganga 2 and Ganga 3 for the plains and Himalaya 123 for the hills, were released. The white grained Ganga 2 was the heaviest yielder and the yellow grained Ganga 3 soon became the most popular in the Punjab and Uttar Pradesh. The latter outyielded Ganga 101 by 7·8 percent. Later came Ganga 5 which excelled Ganga 3 in yield by 20 per cent. EH238 and EH461 gave respectively 18 per cent and 15 per cent more yield than Ganga 101. The former, with an excess yield of 120 per cent over the local variety, appears to be drought resistant. Among the several superior hybrids produced at the I.A.R.I. are 485 and 486 which excelled Ganga 101 in yield by 42 and 51 per cent respectively, but these varieties have the disadvantage of having semi-flint to semi-dent grains. The hybrid varieties give a yield of upto 3,700 kg per hectare against 1,500 kg of the local open pollinated varieties.

The emphasis now is on growing composite varieties which give a yield of 70-80 maunds per acre as compared to the general yield of 20 maunds per acre from local varieties. In these varieties, plant breeders have tried to combine the good qualities of races from India and from distant lands like Mexico, Venezuela, U.S.A., Cuba, Peru, and Colombia. From this "Melting pot" they chose promising superior populations and built them up through careful breeding.

Several composite varieties of maize have been produced in India and those released by the I.C.A.R. in 1967 are Jawahar, Ambar, Vijay, Vikram, Kissan and Sona. The yield potential of these varieties is as high as, and often greater than that of hybrid varieties. Moreover, they possess a greater degree of resistance to pests and diseases and tolerance to drought. Vijay, developed at the Punjab Agricultural University at Ludhiana, gave an average of 4,090 kg. per hectare—a yield 13·7 per cent more than that of

where the rainfall is 50 cm. or more. Its chief advantage lies in its bristled ear which gives it natural protection against bird damage. This tall variety develops 3 to 4 ears per plant and matures in about 90 days. The grain is round and medium sized and on cooking swells more and tastes sweeter than A1/3. It gives 10 to 30 per cent more yield than A1/3. Even under barani conditions this variety outyielded T 55 by 10 per cent.

An outstanding variety released by the I.C.A.R. in 1965 is 'Hybrid Bajra No. 1' for cultivation all over the country. This hybrid was produced at Ludhiana and won Shanti Swarup Bhatnagar award for one of the scientists at the university. It is a cross between Tifton CMS23A, a male sterile line introduced from U.S.A., and BIL-3B isolated at Ludhiana from S530. The hybrid gives about 100 per cent more yield than the previous improved varieties and does well both in irrigated and rainfed areas, though the best results are obtained under irrigated and high fertility conditions. The hybrid is equal to the earlier varieties in dry stalk yield and quality of grain and fodder. On account of its uniform heading and maturity it is less liable to bird damage. It is early maturing, taking about 85 days to ripen, and shows greater resistance to lodging and green ear disease. Another promising hybrid is 23 A×BIL-I. It outyielded T55 by a margin of 79·3 per cent and was second to H.B.I. Two years back (June, 1968) a new drought resistant variety with high yield potential was evolved in Maharashtra.

BARLEY

Barley is a hardy cereal crop of rainfed areas or saline soil, and drought resistant varieties are needed. The earlier approved varieties for semi-irrigated and rainfed conditions were respectively C164 and C138. KB71 was recommended for hilly areas. New varieties BG1 BG18 and BJ29 showed better performance than C164 in irrigated areas. Under barani (rainfed) conditions C167 yielded 117 kg. per hectare more than C138, and BG2 yielded 807 kg. per hectare against 565 kg. of C138, giving an increase of 43 per cent. In the coordinated trials RS6 gave the highest yield of 3100 kg/ha which was 32 per cent more than that of the standard variety. NP113 gave the second highest average.

Varieties for Hill Areas. The emphasis is on the development of rust resistant varieties. New varieties B24, Cul 1-4, Cul 1-5 and

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kg. per hectare against 2,503 kg. of Jhona 349. EK70, an improved variety from Maharashtra, yielded 3,274 kg./ha. This variety has dense earheads and is fine grained but the grains are shorter.

A Basmati type from the hilly region T 23 has been introduced in the plains and has proved superior to Basmati 370. T 23 is a fortnight earlier in flowering than Basmati 370 and yet its yield was 12·5 per cent more than that of the latter.

Some varieties introduced from other states in India and from abroad (Formosa, Iraq and Philippines) have been found to be very promising for the Punjab. Among these are Ac 3400, Ac 3402, and Ac 3404. The last two gave 25 per cent higher yield than Jhona 349, while an increase of 49 per cent was obtained with Ac 3400. These new varieties may replace Basmati 370 and Jhona 349.

In 1966, two very promising varieties introduced from the far east were released by the I.A.R.I. These are 'Taichung Native-1' (T.N.1.), a Formosa-bred variety, and IR-8 developed at the International Rice Research Institute in the Philippines. Both are dwarf and resistant to lodging and give outstanding yield. Under high fertiliser condition T.N.1 gave an average yield of 43.1 gm per plant as compared with 34·6 gm from Jhona 349. The total yield was 70 maunds of paddy per acre. IR-8 was far superior to T.N.1 and Jhona 349 in yield, disease resistance and quality. This miracle rice gives a yield of about 10,000 kilograms per hectare or about 110 maunds per acre. With this variety, Dr. J.P.Patil of the Jawahar Lal Nehru Agricultural University, Jabalpur obtained a yield of 107·5 maunds of grain per acre. With the proper use of farmyard manure and chemical fertilisers, and control of disease and insect pests it has a yield potential of 150 maunds per acre. T.N.1. has lost favour with the farmer for several reasons. It is susceptible to disease and vulnerable to rain and water-logging. It requires high expenditure on irrigation and fertilisers and is not liked by the consumer and fetches lower price. Its fodder yield is less than that of the indigenous varieties. Recently (1968) the Andhra Pradesh Agriculture Department has released a new variety Hansa which is as high yielding as T.N.1. Padma, Jaya and Vijay, and Bas. 217 from Birla Agriculture Farm at Rupar (Punjab) are other new varieties released during 1968-69. Jaya from Bangalore is superior even to IR-8. Among the new varieties released by the ICAR for the current kharif season are Jagannath Pankaj, suitable for water-logged soils and the new hybrids Jamuna and Sabarmati which combine the qualities of Basmati and the high yield of exotic dwarfs.

New Varieties for Hill Areas. At Kulu Norin 18, Norin 12, Asahi, Ch. 972 and Ch. 988 gave considerably higher yield than the recommended variety Dundar 43. The first three varieties belong to the japonica race. Norin 18 was the biggest yielder giving a mean yield of 4,683 kg. per hectare in trials as compared to 2,742 kg/ha of Dundar 43. It has been released for cultivation in the hilly districts of Kulu and Kangra. This high yielding variety has stiff but coarse grains.

'Taichung Native-1' proved superior to Ch. 988 in the hills. A strain produced from an inter-racial cross Norin 18×Ram Jawain gave slightly better yield than the standard R.J. 100. A hybrid from the cross Norin 18×P.P.72 gave 57 per cent higher yield than the standard Phulpattas 72. New introductions Jattu, Norin-10 and China-972 also gave considerably higher yields at Kulu than the standard, Dundar-43. Selections from the crosses Norin 18×Jattu and Norin 18×Dundar 43 gave better performance than Dundar-43 and Norin-18. In Jammu and Kashmir, Bas. 370 is being replaced by China 1039 on account of its low yield.

SUGARCANE

Breeding aims at developing improved varieties which combine high cane yield, high sugar content, good quality and resistance to drought, frost, pests and diseases, besides suitability to different agro-climatic regions. Several new varieties developed at the Coimbatore Sugarcane Breeding Institute have been found to be suitable for the plains and submontane regions of the Punjab and contiguous areas.

New Varieties for the Plains. The standard early variety is Co. L. 29. A new variety Co. 1266 gave the most outstanding performance at Jullundur. At Kheri, P12091 gave the highest yield, followed by Co 1318, both outyielding the standard Co L29, but had slightly less sucrose percentage than Co L29. *G12606* also gave much higher yield than Co L29 and has been released for cultivation.

In the mid season group Co J 76, followed by Co 975, outyielded the standard variety Co L9 at Jullundur by a big margin. Co J76 also possessed higher sucrose content than the other varieties of this group. Co 975 exhibited considerable frost resistance. At Kheri, Co 975 topped the list in yield, followed by Co 1305 and Co 1158. The last two also excelled the standard variety Co. L9 in sucrose content.

The standard variety in the late season group is Co J 46. A new variety Co 1148 (developed from the cross P4383×Co 301) was released in 1967 for the sugar mill areas on account of its persistent all-round performance. Besides being a high yielder and late-ripening, it is erect and non-lodging and highly resistant to frost and moderately resistant to red rot, Gurdaspur borer and top borer. It keeps green and retains its quality till late in the crushing season. It is, however, not suitable for making **gur**.

However, the biggest yielder at Jullundur was Co 62401, followed by Co 740 and P 11996. The first and the last also gave higher sucrose content than the standard Co J 46. At Kheri P 11996 excelled the standard both in cane yield and sucrose content. Co 1236 also significantly outyielded Co. J 46.

Among the **late maturing varieties** Co 1148 was the highest yielder (sugar content 15·6 per cent) at Gurdaspur followed by Co 62401 (sugar content 15·9 per cent) and Co 1236 (sugar content 15·1 per cent). The standard variety C. J 46 (sugar content 15·3 per cent) came last. At Jagadhri P 11996 gave the highest yield, followed by Co 1236, Co 1148 and Co 617.

Recently (1968), a new variety of sugarcane with 22 per cent sucrose content has been developed at Coimbatore.

Submontane Varieties. In the early group, Co 1266 at Yamunanagar and P 12235 at Gurdaspur were the highest yielders. As regards sucrose content Co 1332 topped the list at Yamunanagar and Co 1318 at Gurdaspur, followed by P 12235.

In the **midseason group**, Co1007 and Co975 gave the highest yield, followed by Co 1158 and CoS.245 as compared to the standard CoL9. Co S 245 had 15·1 per cent sugar content and Co 1330 had 14·9 per cent while the standard variety Co-L 9 had 14·1 per cent sugar content.

Several frost-tolerant and red rot resistant varieties also have been developed at Coimbatore. Frost-resistant varieties are Co 1328, Co 975, Co 1148, Co 1330 and Co L 29, Co 1244 proved to be resistant to red rot. Co 975, Co 1107, Co 1148 and Co 1330 showed moderate resistance to this disease. Losses in cane tonnage due to red rot ranged from 14·4 per cent in Co453 to 72·7 per cent in Co 312 while the loss in available sucrose varied from 18·7 per cent in Co 453 to 59·3 per cent in Co. L29. Huge losses are also caused by the smut disease. Varieties resistant to this disease are Co 290, Co 449 and Co 617.

Commercial and disease resistant varieties of sugarcane developed at Coimbatore are now grown all over the world.

GRAM

Improved Varieties for Rainfed Areas. The traditional approved varieties for barani (rainfed) areas are S. 26 and G. 24, the former for areas of low to moderate rainfall and the latter for very low rainfall areas and sandy soil conditions. Breeding is done for resistance to drought and wilt, and for early maturity with high yield.

Several new strains have been developed. The most promising are C 214, H 602, C 57/1, F 33 and C 706. C 214 is the highest yielder and is resistant to wilt, drought and frost. At Hissar, a low rain-fall area with sandy soil, H 154 and H 155 gave respectively 34·1 and 32·7 per cent higher yield than the standard S 26.

Improved varieties for Irrigated and Adequate Rainfall Areas. The previous standard variety is Pb 7, giving an average grain yield of 1255 kg. per hectare. A new variety F 61 gave a yield of 1455 kg/ha, giving an increase of 15·9 per cent over the standard variety, and another variety G 130 gave a still better yield of 1537 kg/ha, giving an increase of 22·5 per cent over Pb. 7. G 130 is resistant to the blight and wilt diseases, has bolder seeds, more seeds per pod and matures earlier than Pb 7. C 214, described in the preceding paragraph, gave higher yield than even G 130.

Blight resistant varieties for humid areas. In the humid sub-montane and hilly areas the crop is subject to blight and wilt diseases. The approved variety for this region is C 235 which is resistant to blight but not to wilt. The new variety G 130 is resistant to both the diseases and is likely to replace C 235.

Improved seed for culinary purpose. The traditional and popular varieties are Kabuli gram and green gram. The former is valued for its bold size and good colour. The old approved variety C 104 of Kabuli gram is susceptible to wilt and blight which cause heavy damage to the crop. A new strain L 144 has now been evolved which gives about 8 per cent more *yield than C 104*, bears much larger seeds and also matures earlier. It is very suitable for Haryana.

New strains of the green gram have also been developed. Of these L 169, L 241, L 242 and L 244 outyielded the Kabuli strain C 104 but none could excel Pb. 7.

COTTON

In India, both long staple American cotton and short staple desi cotton are cultivated. The land under cotton cultivation is two crore acres, the largest in the world. Yet our production is low and

imports have to be made. The I.C.A.R. is stepping up plans for the production and increased cultivation of long staple varieties to cut down our dependence on imports.

Breeding of Long Staple Cotton. Breeding work aims at developing improved varieties of American cotton with mean fibre length of 28·4 mm, better spinning quality and higher ginning percentage. Another desired trait is resistance to Jassid. Early maturity is another desired trait as it saves the crop from frost. The standard variety for Hissar is H14 with mean fibre length of 23·7 mm. In one trial experiment, a new variety H 183 outyielded H 14 by 42 per cent. It had fibre length of 27·3 mm. H 162, with mean fibre length of 29·1 mm also gave significantly (16 per cent) higher yield than the standard H 14 and came next to H 183. In another trial experiment, H-138-13 a promising reselection from AC 138, performed better than H 14 and its own parent AC 138. It had a mean fibre length of 28·2 mm which is very near the set objective. H 138-13 is sympodial in habit, uniform in maturity and matures as early as H 41, besides possessing longer fibres.

The traditional standard variety for Abohar and central Punjab is 320 F, with a mean fibre length of 24·4 mm. In one trial at Abohar, the locally developed variety A 231 performed better than the standard 320 F. A 218 came next to A 231. Both these had a mean fibre length of 28·4 mm. A 231 also outyielded 320 F in trials at Hissar. This strain is very promising. It is strongly sympodial, early maturing and hence safe from frost which was the main scourge of Abohar strains developed earlier.

A new jassid resistant variety of American cotton J34, evolved from the cross 45 F×LSS, has now been released for central Punjab and Karnal district of Haryana. The new variety outyields 320 F by 20 to 30 per cent, possesses superior fibre properties and is less susceptible to Jassid attack.

Several other strains—J 124, J 135, J 136, J 140, and J 148—hold out promise of higher yield than 320 F, combined with superior fibre properties and greater jassid resistance.

Improved Varieties of Desi Cotton. Breeding work is done with the two-fold object of (*i*) developing high yielding, high ginning and harsh stapled varieties and (*ii*) developing high yielding varieties with good lint quality and high ginning outturn.

The old standard variety is 231 R. Two improved varieties G1 and G27 gave considerably higher yield than 231 R. Both these

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In India, both long staple American cotton and short staple *desi* cotton are cultivated. The land under cotton cultivation is two crore acres, the largest in the world. Yet our production is low and

imports have to be made. The I.C.A.R. is stepping up plans for the production and increased cultivation of long staple varieties to cut down our dependence on imports.

Breeding of Long Staple Cotton. Breeding work aims at developing improved varieties of American cotton with mean fibre length of 28·4 mm, better spinning quality and higher ginning percentage. Another desired trait is resistance to Jassid. Early maturity is another desired trait as it saves the crop from frost. The standard variety for Hissar is H14 with mean fibre length of 23·7 mm. In one trial experiment, a new variety H 183 outyielded H 14 by 42 per cent. It had fibre length of 27·3 mm. H 162, with mean fibre length of 29·1 mm also gave significantly (16 per cent) higher yield than the standard H 14 and came next to H 183. In another trial experiment, H-138-13 a promising reselection from AC 138, performed better than H 14 and its own parent AC 138. It had a mean fibre length of 28·2 mm which is very near the set objective. H 138-13 is sympodial in habit, uniform in maturity and matures as early as H 41, besides possessing longer fibres.

The traditional standard variety for Abohar and central Punjab is 320 F, with a mean fibre length of 24·4 mm. In one trial at Abohar, the locally developed variety A 231 performed better than the standard 320 F. A 218 came next to A 231. Both these had a mean fibre length of 28·4 mm. A 231 also outyielded 320 F in trials at Hissar. This strain is very promising. It is strongly sympodial, early maturing and hence safe from frost which was the main scourge of Abohar strains developed earlier.

A new jassid resistant variety of American cotton J34, evolved from the cross 45 F×LSS, has now been released for central Punjab and Karnal district of Haryana. The new variety outyields 320 F by 20 to 30 per cent, possesses superior fibre properties and is less susceptible to Jassid attack.

Several other strains—J 124, J 135, J 136, J 140, and J 148—hold out promise of higher yield than 320 F, combined with superior fibre properties and greater jassid resistance.

Improved Varieties of Desi Cotton. Breeding work is done with the two-fold object of (*i*) developing high yielding, high ginning and harsh stapled varieties and (*ii*) developing high yielding varieties with good lint quality and high ginning outturn.

The old standard variety is 231 R. Two improved varieties G1 and G27 gave considerably higher yield than 231 R. Both these

strains are harsh stapled, short statured, strongly sympodial and hence suitable for cultivation. G1, a reselection from Ganganagar 1, is a high ginner too and it yielded 12·3 per cent more than 231 R. The most promising new strain, however, is the red pigmented G27 which has become popular with the growers by virtue of its persistently much higher yields than 231R (standard) during the years 1963 to 1966. It is a week earlier in maturity, fairly tolerant to water-logging, and other adverse agroclimatic conditions and is fairly resistant to pink bollworm attack. The lint is extra-superfine and *suitable for export.* Another promising harsh stapled high yielder is G57. It excelled even G27 in yield and ginned the highest. G67, a reselection from C250, outyielded 231R by 28 per cent and was conspicuously early in maturing and hence safe from frost. It also excelled G27 and G57 in yield.

TOBACCO

The common cultivated species in the Punjab are *Nicotiana tabacum* (**Desi** tobacco) and *N. rustica*. The old approved variety of **Desi** tobacco is T17 which is a high yielder but of poor quality. In the field trials, new varieties S45, C25, C23 and C29 outyielded T17 by large margins ranging from 23 per cent (C29) to 31·7 per cent (S45). A hybrid 59×165 gave 15·7 per cent more yield than T17 and a selection S35 gave considerably higher yield than T17.

Improved varieties of *N. rustica* (**Kalkattia tobacco**) have also been developed at Ludhiana. A new release C 302 has large, thick and densely placed dark green leaves which are more valued than those of the standard variety T238. The plants are camparatively late maturing and short statured with suppressed inflorescence and low suckering. Its average overall output was 4779 kg/ha against 3714 kg/ha of T238, giving a margin of 28·6 per cent. It is now the standard variety and has replaced T238.

Still better varieties of **Kalkattia tobacco** have been developed. New strains 902/2, and 903/3 from the same cross, 226/4-5×192, outyielded C302 by 19·4 and 16·6 per cent respectively. A new strain C32 excelled C302 by a significant margin of 27 per cent. The hybrid 31×192 outyielded C302 by a big margin. Moreover, this hybrid is more tolerant to Kallar in the soil and salts in the irrigation water and also has slightly higher nicotine content and gives sturdier seedlings with better set on transplanting.



Plate 1. An earhead of wheat before (left) and after mutation (right)

Text reference on page 230] [*To face page 256*

FODDERS*

Natural pastures and cultivated fodders are cheapest source of nutrients required by the cattle for growth, maintenance and milk production. Green fodders are rich in protein and calcium but deficient in phosphorus, which is increased by applying phosphatic fertilizers. They also have plenty of sulphur, potash and magnesium but lack of sodium and chlorine necessitates extra feeding of common salt.

Forests and wastelands in India ensure a sufficient supply of natural grasses like Anjan and Dub, but as more and more of such area is being brought under cultivation and as the dairy industry is expanding, there is a great need for fodder development. In the past, the acute food problem had kept the fodder cultivation neglected and hardly 3 per cent of the cultivated area has remained under fodders, thereby creating a deficit of about 60 per cent in the green fodder supply. With the harvest of bumper crops, self-sufficiency in food has almost been achieved and fodder development is receiving more attention

A good fodder should be quick-growing and high-yielding with high nutritive value. It should be palatable, easily digestible and harmless to the cattle. A low cost of cultivation and regular supply of green fodder are the essential features of a good fodder crop. With the recent researches at the Punjab Agriculture University, Ludhiana, excellent progress has been made in this direction and work done by Dr. V.P. Gupta in the development of new high-yielding and superior quality perennial fodder has been acclaimed highly by the agro-scientists in India and in foreign countries. Farmers have developed a craze for the new hybrid fodder.

Perennial Fodders. The perennial plant types are the best suited for regular supply of green fodder. Elephant grass or Napier grass (*Pennisetum purpureum*), a perennial relative of *Bajra*, was introduced in India in the beginning of this century, but could not become popular because of its low quality. Some past attempts at crossing this grass with bajra resulted in hybrids of intermediate quality. To overcome these shortcomings work on development of superior quality perennial fodders was started in 1964. Extensive study of bajra germplasm, proper choice of parents therefrom and crossing the same with Napier grass has resulted in the development of some very high yielding and superior quality hybrids. These hybrids hold great

*This article has been contributed by Dr. V.P. Gupta, Geneticist, Punjab Agricultural University, Ludhiana.

diploid and tetraploid strains is considered useful. Tetraploid is more suitable for mixed cultivation with NB21, the new Napier-bajra hybrid. Berseem cultivation has almost completely replaced the cultivation of shaftal (Persian clover) and senji (Indian clover).

Oats are grown as a rabi fodder largely on military farms as they are especially suited for horses. They can be fed green or as hay. Four improved varieties recommended by the Punjab Agricultural University are Weston 11, Brunker 10, Algerian 19 and F.O.S. 1129.

Kharif Fodders. Sorghum called *jowar* or *chari* (*Sorghum vulgare*) is the most important kharif fodder as it makes excellent silage. Its dry fodder is the best, but its green fodder is toxic if fed before earing stage, due to the presence of HCN. To improve the nutritive value of this fodder it is fed mixed with leguminous fodders like cowpeas. It is also an important grain crop of India and considerable breeding work has been undertaken to develop disease resistant high yielding types. The fodder types developed by selection are Sundhia, Dhudia, Nilwa, Utavali, Imphi, Maldandi, Dagdi, Kalbondi, Periamanial, Coimbatore 10 and 11, Purbia, J.S. 20, J. S. 21, J.S. 263 and J.S. 29/1. The recently developed grain hybrids CSH1 and CSH2 also give good dry fodder yields.

Maize is also grown as a fodder crop and, unlike jowar, it can be fed at any stage of growth. No specific types have been developed for fodder exclusively, but the newly developed synthetics can be successfully grown as improved fodder types.

Sudan grass (*Sorghum sudanense*) was introduced in India in 1920. It is drought resistant but like sorghum it is harmful due to the presence of hydrocyanic acid (HCN) before flowering stage. Its silage is inferior to jowar but in other respects it resembles jowar. Sweet Sudan 59-3 is recommended by the Punjab Agricultural University. New Sudan hybrids are being developed for high yield and superior quality.

Bajra is the most drought resistant, quick growing, high yielding and nutritious green fodder. Its dry fodder is less nutritious, but the green fodder is far superior to maize and jowar. Local types like Malbandro and Nadam in South and T55 and S530 in North are used for green fodder cultivation. The F_2 seed of H.B.I. and other grain hybrids can successfully be used to get higher green fodder yields. Extensive work has been done in recent years for isolating high yielding and superior quality germplasm of bajra and

it is being used in developing prolific types for green fodder. New types have also been developed at Ludhiana and New Delhi that will give more than one cutting of green fodder.

Cowpea is a kharif legume, generally grown mixed with other kharif fodders to provide a balanced cattle feed. The improved varieties developed by selection are cowpea No. 1, K397 and C57. A new type cowpea No. 10 does better in heavy rainfall areas.

Guara is an important drought resistant fodder but it cannot withstand excessive moisture or waterlogging. Its fodder is coarse and suitable for feeding the draft cattle. Its grain is also highly nutritious and can be fed as a concentrate to livestock except horses. Guara No. 2 is the improved type recommended for general cultivation. A new cluster type Guara No. 277 has been developed at the Punjab Agricultural University, which gives higher returns of both grain and green fodder.

QUESTIONS

1. What are the objectives of plant breeding ?
2. How have variations arisen in crop plants and what is their significance to the plant breeder ?
3. Describe the role of selection in plant breeding. Describe the principal types of selection.
4. Describe the procedure of hybridisation and selection as used in self-pollinated crops.
5. Describe the following methods of plant breeding : [illegible] method [illegible]
6. [illegible]
7. [illegible]
8. What are hybrid varieties ? Describe the procedure employed [illegible] development of hybrid varieties of maize.
9. Compare the following methods of selection as applied to cross-pollinated crops :
   (*a*) Progeny selection. (*b*) Recurrent selection (*c*) Mass selection
10. Describe the procedure of breeding asexually propagated plants.
11. Write comprehensive notes on :
    (*a*) Mutation breeding, (*b*) Polyploid breeding, (*c*) Composite varieties.
12. Name two allopolyploid crop plants and describe their evolution.
13. How are disease resistant varieties of crop plants developed ?
14. What is meant by improved varieties of crop plants ? What is their significance ?
15. Give a brief account of plant breeding work in India with reference to any two major crop plants.
16. Name two varieties of Mexican wheat introduced in India in recent years. Give their genetic and agronomic characters. Give an account of the new varieties developed in India from this imported stock.

14

EVIDENCES OF EVOLUTION

WHAT IS EVOLUTION

MAN is a supreme being and by nature inquisitive. Gifted with the faculties of thinking and reasoning, he has always tried to understand the "how" and "why" of the natural phenomena that come under his observation. An important natural phenomenon that attracted the attention of man long long ago was the great diversity of forms among plants and animals. How these thousands of different kinds of plants and animals came into existence is a question which thinkers of all ages have attempted to answer. When and where this question arose in the mind of man first need not concern us here. Suffice it to say that the question is centuries old and there are references, some direct and some indirect, relevant to this problem in the writings of the ancient Greeks and in the mythology of the east as well as the west.

The ancient people supposed that all the varied forms of plants and animals that live today have been there since the beginning of this world and will continue to live unchanged till eternity. These had been made outright by some divine power and have come down to our times after the lapse of millions of years in the same form in which they were first created. This is the theory of **special creation**, according to which each type was created as a separate and fixed entity incapable of changing or giving rise to other kinds of living organisms. Most men subscribed to this view. Such an idea still persists in the minds of some people, though they are not numerous. But there were others, only in insignificant minority, to whom the idea of special creation did not appeal. To them, the different degrees of resemblances, which they observed in the various types of plants and animals, were very striking. This suggested relationship. The discovery of fossils was a remarkable event. It was

discovered that the plants and animals which had inhabited the earth in the different periods of its history had been far from similar. The organisms that lived in any particular period were very different from those of the earlier or the later periods. The changing pattern of organic life as written in the rocks of the earth was explained by the advocates of the theory of special creation by supplementing it with the theory of catastrophism. This theory assumed that the earth was visited periodically by catastrophes which destroyed all life from time to time, each catastrophe being followed by new and specially created forms of life. As our knowledge of fossil plants and animals increased, it became apparent that the number of catastrophes necessary to account for the known succession of floras and faunas was absurdly large. Further, this theory would require that all forms of life that lived at the time of any catastrophe were destroyed simultaneously. Fossil record gives no evidence of such a wholesale destruction. On the contrary, it indicates that the change was gradual and spread over a long period ; each form appeared, flourished, then gradually declined and finally disappeared. All this happened gradually in the course of millions of years.

There is an alternative explanation to account for the above phenomena. The plants and animals that have inhabited this earth have been changing in the different periods of the earth's history. In the beginning there were simple types of organisms and from them all the varied and more complex types of plants and animals have been derived. In other words, the present-day plants and animals have descended from simpler forms that existed on the earth in former times. This change has taken place in an orderly fashion, so that the nature of each change is influenced by what has gone before and in turn determines the nature of the next change. This process of orderly change by which the various species of plants and animals of today have descended with modification from those of the past is known as **organic evolution**. Evolution usually results in the production of more complex forms of life from comparatively simple predecessors, and is said to be progressive. Occasionally, simpler forms arise from more complex ones in which case evolution is said to be retrogressive. The plants and animals which existed earlier in the earth's history are said to be primitive and those that came later are said to be advanced.

The definition of evolution given above is only in general terms, and does not imply any particular line of descent for any particular species. Evolution is going on even now as it has been going on in

the past. Plant and animal species of today are descended from different and in most cases simpler kinds of life that lived in the past and will in course of time produce new types of plants and animals.

EVIDENCES OF EVOLUTION

That evolution has occurred among plants and animals is now a matter of belief with biologists all the world over. In fact, the doctrine of evolution is one of the most important scientific generalisations. This belief has not arisen because we can point our finger and say 'here is evolution taking place'. Evolution is a very very slow process which cannot be observed as we can observe things and events around us. The process of evolution was compared by Lamarck (1809) to the slow movement of the hour hand of a clock. A creature whose life-time was only one second would not perceive any motion in the hour hand. In evolution, time is reckoned not in terms of years and centuries but in terms of aeons (geological time scale) and man is in no better position than the creature mentioned above. This belief in evolution has been arrived at as an inescapable conclusion from an enormous amount of circumstantial evidence derived from several sources. On the basis of evolution, numerous observed facts and phenomena of nature can be reasonably explained but which would otherwise cause wearisome confusion. The similarities and dissimilarities of living things are meaningless from any other standpoint than that of evolution. The various lines of evidence in favour of this doctrine of evolution of species and the various observed facts which this doctrine can explain, but which could not be adequately accounted for on the basis of other imaginable causes, are briefly described below.

EVIDENCE FROM CLASSIFICATION

Plants and animals show a great diversity of form. They also show some similarities amongst themselves. It is on account of these differences and resemblances that the taxonomists have been able to arrange the living things into smaller and larger groups. Thus, the taxonomists have recognised that there are about 250,000 different kinds of plants. These different kinds are called species. The members of each species are recognised by their close resemblance to one another, their differences being of a minor type. Amongst species also there are differences and resemblances of

The natural system of classification follows the branching pattern of a tree, from the phylum to the genera and species. In this tree of classification, the species, genera and families, etc. are comparable to the leaves, branches and larger branches, all ultimately springing from the common stock. This conception is not practical on the basis of special creation because here a tree is made of independently created leaves, twigs and branches which are then artificially jointed.

The ultimate unit of classification is the species. Taxonomists are not fully agreed as to the definition of species. Sometimes, forms described as one species by one taxonomist are divided into two species by another. Sometimes, it cannot be definitely said whether a particular species belongs to this genus or that. The same difficulty may arise in the allocation of genera to families, and also sometimes in the case of higher groups. Such situations are responsible for the adoption by different authorities of different systems of classification.

A species is an assemblage of all individuals of one kind, resembling one another in most of their qualities and differing from one another only in minor details ; it is sharply separated from all other species in one or more respects. All the members of a species are mutually fertile and either infertile with other species or else only produce partially or wholly sterile hybrids. Interspecific fertility is very rare. Different species are often geographically separate, although their ranges may sometimes overlap.

EVIDENCE FROM FOSSILS

The plants and animals that lived in the remote past have in many cases left proofs of their existence in the form of remains in the rocks. These are called **fossils**. The study of fossils provides the most convincing and direct evidence of evolution. Before discussing the evidence offered by the fossils, it is necessary to know something about the rocks, their ages and the manner in which fossils were formed.

The rocks. A rock is an aggregation of minerals. It may be made up entirely of a single mineral as in rock salt, but more often it contains two or more minerals. Granite, *e.g.*, is composed of feldspar, quartz and mica. Rocks form a part of the earth's crust. They are abundant beneath the surface of the earth where they form large beds at different depths. Sometimes, they are exposed in such places as cuts made for highways or railroads,

along deeply cut stream banks, in quarries, or sometimes, out-cropping on the slope of a mountain.

Rocks are of three principal kinds, depending on their origin, their position in the earth's crust, and their location with respect to each other. These three types are sedimentary rocks, igneous rocks and metamorphic rocks.

Sedimentary rocks were deposited by water or winds assisted by the force of gravity and occur in the beds of oceans and other large bodies of water, or in deserts. We have described in chapter 2 how moving water that flows down the mountain slope or in the plains during or after a heavy rain carries along with it much suspended material that gradually becomes finer and finer. When the water is quiet, the sediments begin to settle down, forming deltas or they may settle on the bottom of the ocean or lake into which the streams flow. Later on, this sediment hardens into rock. As more sediments settle down and harden, they form successive layers or strata of rocks. Some common examples of sedimentary rocks are limestone, shale and sandstone ; iron ore beds, coal and rock salt are included in this group.

Igneous rocks are formed by cooling of the materials forced up by volcanoes from the earth's interior. The molten lava does not always reach the surface of the earth before cooling. These rocks are not stratified but crystalline. The portions cooling at or near the surface of the earth have smaller gr[illegible] those far below, in which the cooling process is more slo[illegible] [illegible] the most common igneous rocks and is used ext[illegible] purposes and for monuments.

surface have been laid down. In the identification of particular strata, the fossils that they contain are also helpful.

The determination of geological time in terms of years is not possible with the above method. Better and more accurate methods for the determination of geological time in absolute units of measurements—years, lakhs or crores of years have now been developed, based on the spontaneous disintegration of radioactive elements. Radioactive Uranium (at. wt. 238), *e.g.*, slowly disintegrates to produce Lead (at. wt. 206) and Helium. The rate of this disintegration is invariably constant and independent of other external conditions. It will require 4,510,000,000 years for half of the atoms of any mass of Uranium to change to Lead and Helium. This figure is independent of the actual quantity of Uranium originally present, and is called the "half" life of the element, that is, the time in which a certain number of its atoms will decay to half its value. From the amounts of Uranium and Lead present, the time that has passed since the formation of the rock can be calculated. Other isotopic transformations, besides the conversion of uranium to lead, are also used for measuring geological time, for example, the conversion of Thorium 232 to lead, potassium 40 to Argon, Rubidium to Strontium and Carbon 11 to boron. The time-table worked out with the help of rubidium and potassium 'atomic clocks' has been found to be more accurate. The age of the oldest rocks in India, South Africa and U.S.A. is about 3·5 billion (350 crore) years. The earth itself must be still older since it must have taken a considerable time for the rocks to be formed out of the hot gaseous mass with surface temperature of 6000° to 8000°C as a result of cooling. The age of the earth as measured by Patterson by the so-called lead method is 4·5 billion (450 crore) years. The age of our sun, which is a star and of which our earth is one of the planets, is about 5 billion years. The rocks of the earth that bear signs of life are about 2 billion (200 crore) years old. Prior to this, conditions on the earth were unsuitable for life. The period earlier than this is, therefore, called azoic.

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Metamorphic rocks mean changed rocks. They are formed from the other two groups by processes which have changed their texture and mineral composition. They may have changed or they may have been made stronger by the process. The processes which have changed them are weight, heat, movement and pressure in the presence of water and gases. Some common metamorphosed rocks are slate formed from clay ; marble from limestone ; quartzite from sandstone ; and anthracite coal from soft coal.

Rock formation has been going on since the beginning of the earth. Several methods have been developed to determine the age of different rocks. In the case of sedimentary rocks, the deepest strata are the oldest while the most superficial are quite recent. This method only gives the comparative dating of rocks. It is possible to determine the sequence in which the various strata of the earth's

surface have been laid down. In the identification of particular strata, the fossils that they contain are also helpful.

The determination of geological time in terms of years is not possible with the above method. Better and more accurate methods for the determination of geological time in absolute units of measurements—years, lakhs or crores of years—have now been developed, based on the spontaneous disintegration of radioactive elements. Radioactive Uranium (at. wt. 238), *e.g.*, slowly disintegrates to produce Lead (at. wt. 206) and Helium. The rate of this disintegration is invariably constant and independent of other external conditions. It will require 4,510,000,000 years for half of the atoms of any mass of Uranium to change to Lead and Helium. This figure is independent of the actual quantity of Uranium originally present, and is called the "half" life of the element, that is, the time in which a certain number of its atoms will decay to half its value. From the amounts of Uranium and Lead present, the time that has passed since the formation of the rock can be calculated. Other isotopic transformations, besides the conversion of uranium to lead, are also used for *measuring geological time, for example, the conversion of* Thorium 232 to lead, potassium 40 to Argon, Rubidium to Strontium and Carbon 11 to boron. The time-table worked out with the help of rubidium and potassium 'atomic clocks' has been found to be more accurate. The age of the oldest rocks in India, South Africa and U.S.A. is about 3·5 billion (350 crore) years. The earth itself must be still older since it must have taken a considerable time for the rocks to be formed out of the hot gaseous mass with surface temperature of 6000° to 8000°C as a result of cooling. The age of the earth as measured by Patterson by the so-called lead method is 4·5 billion (450 crore) years. The age of our sun, which is a star and of which our earth is one of the planets, is about 5 billion years. The rocks of the earth that bear signs of life are about 2 billion (200 crore) years old. Prior to this, conditions on the earth were unsuitable for life. The period earlier than this is, therefore, called azoic.

Geologists have divided the 200 crore years of earth's history into five major units or Eras shown on pages 270—271. The Eras are divided into periods and periods into epochs. The figures of ages given in the table are only estimates and may have to be revised. The table is, however, valuable from the point of view of the comparative ages of the rocks, the oldest period being placed at the

bottom and the most recent at the top. The table also gives information about the flora and fauna of the different periods.

Fossilisation. When organisms die, their dead bodies in most cases are decomposed by bacteria or fungi or else are destroyed by predators or scavengers. Sometimes, a dead body or its parts may escape this fate and may be preserved as a fossil. The best method of fossilisation is burial and the most favourable conditions for fossilisation are met with in the oceans. Decay is checked by salt water. In the oceans live many animals which secrete shells, and there are fishes with bony skeletons. When these animals die, their hard parts settle to the bottom where they are covered with sediment and are protected from scavengers and oxidation. Later on, they remain buried in the rock that forms from the sediment and are preserved as fossils. With further settlement of sediment, the depth of the fossil increases, and hence, in a general way, the oldest fossils may be expected to be found in the deepest layers of the earth's crust while the more superficially located fossils may be regarded as recent in origin. In some instances, the body of a land organism has been washed out to sea and preserved there.

Dust storms have a similar effect on land plants and animals. Desert forms may be dried out by the hot, dry desert winds, and then buried under the shifting sands.

Organisms may be buried under lava flowing from volcanoes and preserved as fossils. Perfectly preserved fossils of whole families, together with their domestic animals, have been found in Pompeii, which was buried under the lava from Mount Vesuvius in 79 *A.D.*

A special method of burial occurred in South California in America. There, springs of petroleum turned into pools of sticky tar after the evaporation of more volatile oils. Many animals, including mammals and birds, were caught in this asphalt and are some of the best preserved of fossils.

Sometimes, insects were entrapped in amber, a yellowish fossil resin. As it dried and solidified, the insects remained embedded in the resin as remarkably well-preserved fossils which show even histological details much like the freshly preserved specimens.

In some fossils, some of the original portions of the organisms have been replaced, at least in part, by minerals dissolved in the water. This process is called petrification. Most of the fossils from sedimentary rocks are of this type. The best example is afforded by the petrified forests of the United States. Petrification usually preserves only the hard parts of the organisms.

Sometimes, parts of plants or animals leave their impression in mud or sand. The body later decays or is removed in some manner but the impression still remains and becomes permanent when the soft mud or sand hardens into stone. These impressions are known as **moulds**. The method works equally well with soft and hard structures. Footprints and leafprints were formed in this manner. In many cases, the cavity of the impression may be filled with some hard mineral resulting in a fossil called a **cast**. Many organisms are known only from the casts and impressions which they have left

From the above account the reader would now be clear as to what is meant by a fossil. A fossil may be defined as an organism or anything indicating the former presence of an organism which has been preserved in any natural deposit in or on the earth's crust. Leafprints, trails of animals, tracks of dinosaurs or burrows of worms are also considered as fossils.

Fossils reveal much interesting earth history and have been employed to determine very definitely the age of the rock strata in which they occur ; they also indicate the factors of the environment in which the plant or animal lived—whether the atmosphere was moist or dry, cool or warm, whether the water was fresh or salty.

Incompleteness of the fossil record. According to the doctrine of evolution, the present-day plants and animals have descended from the simplest forms of life, that lived on this earth in the beginning, by a long but continuous process of progressive change. It naturally follows from this that the fossil record beginning from the earliest to the recent would show a continuous and unbroken series of intermediate forms between the oldest and the recent forms. The story of evolution would be easy to read, and most evident and convincing. Unfortunately, this is not so because of the incompleteness of the fossil record itself and the meagreness of man's knowledge of whatever fossils there are.

There are several reasons for the incompleteness of the fossil record. Only an infinitesimal fraction of the organisms of the past has been fossilised. Most of the dead bodies were destroyed even before taking the first step towards fossilisation as a result of decay or by predators and scavengers, or by water and air. Soft organisms were rarely preserved. Many groups of plants and animals are, therefore, not represented in the fossil record. In others, certain parts escaped fossilisation because they were soft. In plants, for example, only the woody parts are preserved but the flowers which

TABLE 14.1

GEOLOGICAL TIME-TABLE*

Eras	Periods	Epochs	Duration in millions of years	Millions of years ago to the present	Important plants	Important animals
Cainozoic (Age of Angio-sperms and Mammals)	Quater-nary	Recent	0 025	0 025	Decline of woody plants ; rise of her-baceous ones.	Age of man Modern mammals, man domi-nates.
		Pleistocene	1	1	Great extinction of species.	Extinction of great mammals ; first human social life.
	Tertiary	Pliccene	10	11	Decline of forests ; spread of grasslands ; Monocotyledons developed.	Man evolved from man-like apes ; elephants, horses, camels almost like modern species.
		Miocene	15	26		Mammals at height of evolution ; first man-like apes.
		Oligocene	10	36	Maximum spread of forests ; rise of mono-cotyledons.	Early mammals extinct ; rise of arthropods ; forerunners of most living genera of mammals
		Eocene	19	55		Placental mammals diversified and specialised ; hoofed mammals and carnivores established.
		Paleocene	15	70		Spread of early placental mam-mals and modern birds.
Mesozoic (Age of Gymno-sperms and Reptiles)	Cretace-ous		60	130	First. monocotyled-ons ; oak and maple forests ; gymnospe-rms declined.	Dinosaurs reached peak, became extinct ; toothed birds became extinct ; first modern birds; early mammals common.
	Jurassic		35	165	Increase of dicotyle-dons ; cycads, conif-ers, ferns common	First toothed birds and lizards ; dinosaurs larger and specialised ; insectivorous marsupials.
	Triassic		35	200	Gymnosperms domi-nant , decline towards end ; extinction of pteridophytes & seed ferns; no angiosperms.	First dinosaurs and egg-laying mammals ; extinction of primitive amphibians.

Palaeozoic (Age of Ferns and Amphibians).	Permian		30	230	Decline of lycopods and horsetails.	Many ancient animals died out; mammal-like reptiles: modern insects arose.
	Pennsylvanian		20	250	Great forests of seed ferns & gymnosperms.	First reptiles; insects common; spread of ancient amphibians.
	Mississippian		30	280	Ferns, lycopods and horsetails dominant; gymnosperms increasingly widespread.	Insects increase. Amphibians develop rapidly; spread of ancient sharks.
(Age of Aglae and Fishes)	Devonian		50	330	First forests, ferns well-established; seed ferns and first gymnosperms	amphibians; fishes wide l, lung fishes, sharks abun-
	Silurian		30	360	First land plants with stele; algae dominant.	ie arachnids dominant, scor- and spider (wingless) insects; fishes.
(Age of Interteb-rates)	Ordovician		70	430	Seaweeds abundant.	ishes, corals, trilobites and ks abundant.
	Cambrian		90	520	Seaweeds.	brates; only shelled s. Trilobites, brachiopods int ?
Proterozoic			1500?	2,000?	Primitive aquatic plants—algae, bacteria.	protozoa; towards end, :s, worms, other marine brates.
Archaeozoic			???	???	No recognizable fossils deposits of graphites and	ct evidence of life from matter in rock.

*Adapted from Villee (Biology. the human approach), with some modification relating to years, after Colbert.

are the most important to the taxonomist have not been preserved in most cases. Most of the fossils are of marine origin because the sea was the most favourable site for the deposition of rocks and formation of fossils. Most of the land plants and animals are poorly represented in this fossil record.

Rocks together with the contained fossils have been altered or destroyed during the course of earth's history. Rocks crack by tension. The deeper rocks are subjected to increasing pressure and consequent heat as a result of further deposition of rocks above them, thus causing their metamorphosis and recrystallisation, and the loss of contained fossils. Rocks were exposed when mountains were thrust up as a result of periodic upheavals in earth's history ; in other cases, the moving glaciers carried away the superficial strata and laid bare the deeper ones. The exposed rocks were later on eroded by wind and water. In many cases, rivers cut deep gorges through successive strata of rocks. All these processes were accompanied by the destruction of fossils.

In view of all this, it is not surprising that the fossil record is only fragmentary and does not give a complete picture of evolutionary progress. Superimposed upon this is man's limitation. He has thus far discovered and studied only an infinitesimal fraction of the fossils that there are. In spite of these handicaps, fossils are met with in such great abundance in some places that they present a fairly clear picture of gradual and progressive change through successive strata of the rocks

Evaluation of the fossil record Bearing the above facts in mind, we may now attempt some evaluation of the fossil record for various animal and plant groups. In doing so, the geological time-table given on pages 270—271, which relates to the last 200 crores years when life is supposed to have begun on this earth, should be constantly referred to. For about 250 crore years prior to this, conditions were unfit for life. Hence this long period is described as **azoic**. The first two Eras of the earth's history are called **Archaeozoic** and **Proterozoic** or the Eras of Early Life. Together they lasted for about 150 crore years. That is they accounted for three-fourths of the total history of living things on the earth. No fossils are known for the Archaeozoic Era. The only indication of plant life in this era is derived from the occurrence of graphites and limestone. The first plant fossils appear in the Proterozoic and these were of *bacteria* and algae, probably blue green. The representatives of the animal



Plate 3. Life on the floor of a Cambrian sea: trilobites, worms, starfish, sponges, crustaceans, medusas and seaweeds

Text reference on page 273] [*To face page 272*

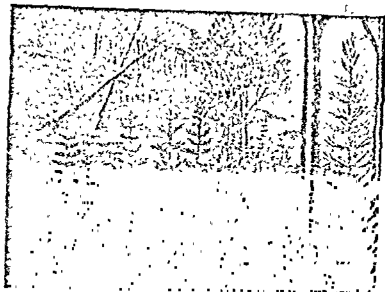


Plate 4. Carboniferous forest of horse-tails ferns
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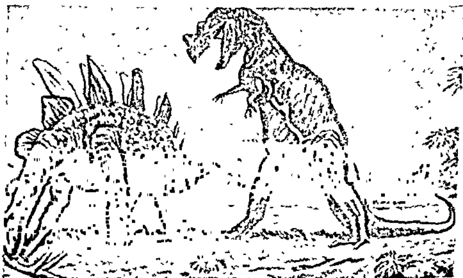


Plate 5 Dinosaurs of the Cretaceous period : herbivorous stegosaur (left) and predatory ceratosaur (right)
Text reference on page 274]



Plate 6. Flying reptiles of the Jurassic period : nude pterodactyl (lower left) and feathered archaeopteryx, progenitor of birds

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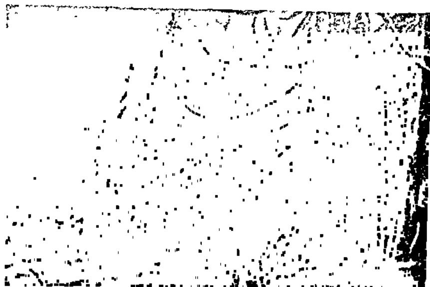


Plate 7. Palm and coniferous forest in the later half of the Tertiary (Cainozoic) period

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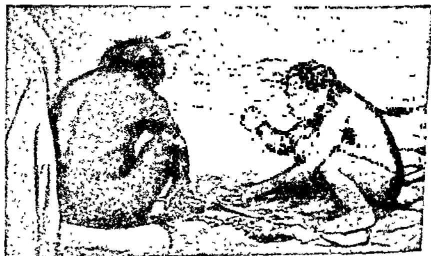


Plate 8. Early man chipping flints to make primitive tools

Text reference on page 275] *[To face page 273*

world were marine protozoa, molluscs, worms and a few other invertebrates. All of these lived in sea water. This early period is also called the **Protozoic Era**

Next came the **Palaeozoic** Era or the Era of Ancient Life. This lasted about 32 crore years In the early part of this Era much of the world was covered with large oceans filled with seaweeds and invertebrates like trilobites, brachiopods, corals, sponges and snails. The invertebrates were the dominant forms of animals both as regards number and diversity. The early Palaeozoic is, therefore, known as the **Age of Invertebrates.**

The land plants appeared only in the Silurian period (middle of the Palaeozoic Era), and the Devonian period is characterised by a great outburst of land plants with woody structures The dominant plants were the ferns and fern-like plants, tree-like lycopods (club-mosses), and giant horsetails (Equisetinae). The Devonian also contained plants of the gymnosperm type. An important group of plants that appeared in the Devonian period was that of the seed ferns (*Pteridosperms*). These were fern-like plants that bore seeds. This interesting group of fossil plants combines the characters of ferns and gymnosperms and throws light on the origin of seed plants. The gymnosperms are regarded as having arisen from the fern ancestors *via* the seed-ferns.

The middle Palaeozoic period also witnessed a great outburst of animal life. The vertebrates appeared for the first time. *They were fish-like to begin with and these gradually blended into* the true fishes. Gradually the fishes became dominant, being the most numerous and of the greatest variety. The mid-Palaeozoic period is, therefore, known as the **Age of Fishes.** The first amphibians also made their appearance at this time.

In the later part of the Palaeozoic (Mississippian and Pennsylvanian periods together called the Carboniferous period), the ferns and fern-allies increased and formed large forests. Large forests of seed-ferns also occurred about this time. The gymnosperms also increased.The ferns and fern-allies began to decline as the Palaeozoic era came to an end.

Large numbers of animals, both invertebrates and vertebrates, began to migrate to land about the end of the mid-Palaeozoic Era. Many of them were able to live both in water and on land. These amphibians which had begun in the Devonian period and resembled salamander and sharks gradually increased in number and in the Carboniferous period were the most dominant animals. The late

Palaeozoic period is, therefore, known as **the Age of Amphibians.** Gradually the amphibians began to decline and insects and reptiles began to appear.

The Palaeozoic Era was followed by the **Mesozoic Era** or the Era of Medieval life. This started about 20 crore years ago and lasted for about 13 *crore years. The pteridophytes and seed ferns now* declined and became extinct. The gymnosperms increased very much. The cycads appeared and flourished in the Triassic and along with the conifers formed large forests and became dominant. About the later part of the Mesozoic, the gymnosperms declined and were gradually replaced by the angiosperms. Today they occupy only an inconspicuous position in the vegetation. The angiosperms increased in number and many trees appeared. There were large forests of oaks, maples, beeches, elms and poplars with grasses in the open, about the end of this era in the Cretaceous period.

On the animal side, the insect population increased in a large way. But the most important animals of this era were the reptiles, a new type that replaced the amphibians of the late Palaeozoic. The reptiles, which had made a modest appearance in the Carboniferous period of the Palaeozoic Era gradually increased and attained a great diversity during the Mesozoic Era. They reached their climax in the Cretaceous period. Most prominent were the giant reptiles, called the dinosaurs (GK. *Deinos* fearsome and *sauros* lizards). They lived everywhere, on land, in the sea, and in the air. While some *were of the size of a hen or a dog, others were of huge size.* Some of the largest dinosaurs weighed upto 50 tons and measured 150 ft. in length. Many of them were odd looking with armour plates over the head or neck or plates of large spines on their back or sides. *Some were flesh-eaters and hornless, and others were* herbivorous and had long horns for self-defence. *Brontosaurus*, the thunder lizard, was a 70 ft. long hornless herbivore without armour. The dinosaurs remained masters of the earth for more than 10 crore years. *Hence the Mesozoic Era is known as the* **Age of Reptiles.**

During the later part of the Mesozoic Era were evolved the birds and the mammals. The first fossil bird of this time is *Archaeopteryx*. This fossil which *is of the size of a crow, is very interesting as it* combines the character of reptiles and birds both (Fig. 14.1). Like the reptiles, it had a long tail with vertebrae and a jaw full of teeth. Like the birds it had clawed wings made of feathers. While modern birds *have a short tail with fan-like feathers,* the tail feathers of

Archaeopteryx were arranged in a row on each side of the tail along its whole length. *Archaeopteryx* is thus a connecting link between the birds and the reptiles. It shows that birds were evolved from the reptiles.

About the end of the Mesozoic Era, the early flowering plants and the early mammals appeared on the scene. The dinosaurs gradually disppeared and became extinct.

The final and the modern era is called the tertiary or **Cainozoic*** **Era**, in which we live. It began about 7 crore years back. The reptiles, which had begun to die in the Cretaceous period at the end of the Mesozoic era, were now gradually replaced by mammals and birds, two highest classes of vertebrates The mammals increased enormously and became dominant. Like their reptile ancestors, the mammals lived everywhere, on land, in the air, in the sea. This era

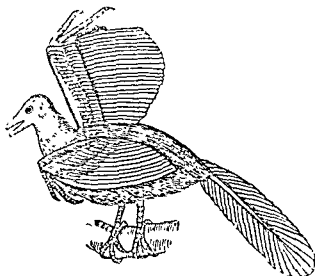


Fig. 14.1 *Archaeopteryx*, the fossil bird of the late Mesozoic Era (Jurassic period)

is, therefore, known as the **Age of Mammals**. The most recent part of this era is known as the **Age of Man** who is undoubtedly the most dominant animal on earth today. The mammals appeared last in evolutionary history but they appeared long before they became dominant.

A great outburst of flowering plants also occurred in the Cainozoic Era. Forests increased and spread everywhere. Later on ensued a period in which the forests began to decline and were gradually replaced by grasslands which began to spread. The herbaceous habit

*Cainozoic (Keno zoic) is also written as Cenozoic (Se-no-zoic).

in angiosperms was the last to develop and gradually attained a dominant position, which position is still maintained.

From the above account we may now attempt some generalisations. Until the Devonian period, all the fossils are of aquatic plants, mostly marine algae. It appears, then, that land plants appeared about 200 million years after the appearance of large marine plants. This is in agreement with the presumed origin of life in the sea. Another point that emerges from the above description of fossil sequence is that the earliest land plants were of a primitive type and the more elaborate types of vascular plants like the gymnosperms appeared much later in the geological time-scale, and the angiosperms appeared last of all. In most major groups, there is marked change from one geological period to the next and there is greater similarity between the flora of the two periods that are near each other in time than if the periods are remote from each other. Finally, the fossils of recent times blend into our present living flora, with several common genera and even common species.

The gradual change in the flora of different periods speaks loudly against fixity of species and special creation. Species appear, flourish and then become extinct, their place being taken by new species that are adapted to the conditions then prevailing. The new species follow the same course as their predecessors and the ultimate fate of all species is the same *viz.* extinction and replacement by new ones. This is evolution.

An important fact revealed by the study of fossils is that the inhabitants of a given period are descended not from all the inhabitants of earlier periods but only from a part of them. Many creatures disappeared from the scene without leaving any descendants.

The same is true of the animal world. It is quite clear that the simplest animals appeared in the most remote geological periods, while the most complex appeared late in geological history. The changing pattern of living creatures through successive periods of geological history can be explained on the basis of organic evolution and entirely rules out any theory of special creation.

In several cases the fossil study gives a clear and a complete picture of evolution of certain plants and animals. The intermediate stages or the connecting links are well preserved as fossils. An example of this is the evolution of the modern horse. The modern horse belongs to the genus *Equus*. Its evolutionary history began in the Eocene epoch in the modern Era about 50,000,000 years

back. The descent of the modern horse (*Equus*) is traced back to *Eohippus* which lived in North America in that age. The gap between *Eohippus* and *Equus* is a very big one. The former animal was no taller than a medium-sized dog. Each of its front feet had four toes, representing the second to the fifth digits. Its hind feet had only three toes. Each toe ended in a separate hoof-like nail (Fig. 14·2). Its molar teeth were constructed for a browsing habit. Two crore years later appeared another animal called *Mesohippus* which

NAME OF HORSE	SIZE	FEET
EQUUS	MODERN HORSE	runs on 1 toe, second and fourth toes have become splint bones
MERYCHIPPUS	SIZE OF AN ASS	had 3 toes but ran only on 1 toe, side toes did not touch ground
MESOHIPPUS	SIZE OF A GOAT	ran on 3 toes, fifth toe reduced to a splint
EOHIPPUS	SIZE OF A FOX	ran on 4 toes, first toe undeveloped

Fig. 14.2. Evolution of the horse from a four-toed animal to the modern horse through the ages. The numbers on the figures in the last column correspond to the numbers of fingers on the hands of man

lived in North America during the Oligocene epoch. It had three toes on each foot with the lateral toes still partly functional. The *Mesohippus* was taller than the Eohippus. It was of the size of a goat. One of the several descendants of *Mesohippus* was *Merychippus* which appeared about one crore years later in the Miocene epoch. It was of the size of the modern ass and had three toes but only the middle one was functional. The teeth had also changed in character so that they could perform chewing movements and were adapted for grazing on grass instead of browsing on twigs and leaves. This switchover from browsing to grazing habit was a critical event that played an important role in the survival of the animal. For at that time in the history of earth, climatic changes were taking place and grasslands were fast spreading and forests were declining. Naturally, the animals which could feed on the harsh grass would have better chances of survival. But this shift to the grasslands also exposed the animal to greater dangers from the predators because it could be seen by the carnivorous animals from a greater distance than in forests. Consequently, natural selection produced stronger and faster grazing animals. While the slow-footed browsers became extinct under the changed conditions, the fleet-footed grazer *Merychippus* survived and left descendants, one of which was *Pliohippus* in the Pliocene epoch. In this animal the side toes were finally lost leaving just a single toe on each foot. *Equus*, the genus of modern horses, zebras and asses, seems to have descended from *Pliohippus*. It appeared first as a fossil about 5 lakh years ago. It has only one toe on each foot and the two side toes are reduced to splint bones.

This story of the horse through the ages illustrates the way by which animals and plants are evolved. The various animals named above are links in the whole series from the little *Eohippus* to the modern horse. The story of the evolution of the modern camel and elephant is also written in the rocks. In their case, also, whole series of intermediate connecting links have been discovered among fossils.

From the above account it should not be construed that the evolution of the horse took place in a direct line form *Eohippus* to *Equus* through the genera mentioned above. The record includes several other genera which were developed at several levels in this evolutionary series. Many of them migrated to Europe, Asia and Africa at various stages and there finally became extinct.

The drama of the evolution of the horse was enacted in North America but the last act in this drama is very puzzling. The *Equus* spread from its home land to Europe, Asia and Africa where it gave

ise to several species of horses, asses and zebras but it ultimately ecame extinct in the land of its birth and was reintroduced into America from Europe by European settlers. The causes that led to he extinction of *Equus* in North America are not definitely known.

QUESTIONS

1. What is meant by 'organic evolution' ? Give three arguments to convince a layman that evolution has taken place
2. What are fossils ? How are they formed ?
3. What light does the study of fossils throw on the concept of evolution ?
4. Describe the flora and fauna of this earth through the ages
5. Discuss the evolution of the modern horse.

15

EVIDENCES OF EVOLUTION (Contd.)

EVIDENCE FROM GEOGRAPHICAL DISTRIBUTION

ANOTHER *line of evidence for evolution is derived from the study of* the geographical distribution of plants and animals, both fossil and present, throughout the world.

During the course of his exploratory voyage on the British Navy ship Beagle, Darwin visited in 1835 the Galapagos Islands, situated about 600 miles off the west coast of South America. He was struck by the endemic nature of most of the plants and animals of these islands. These were found nowhere else in the world. Not only did they differ from the inhabitants of South America but the species of the different islands were often different. To take an example, every island had its own Giant Tortoise which differed somewhat from that on any other island and the tortoises of the various islands differed still more from those of the mainland.

Darwin explained the endemic species of Galapagos on the assumption that they were more or less modified descendants of immigrants from the South American continent. It was an obvious case of the process of evolution. These endemic species do not make sense on any other ground. Galapagos belongs to a class of islands called oceanic islands. *Oceanic islands* have not been connected with any continent or were so [illegible]ted only lo[illegible] [illegible]e Galapagos Islands were thrust [illegible] [illegible]e bottom [illegible] [illegible]n as a result of a volcanic eruption. [illegible] [illegible]on of suc[illegible] [illegible]lated from large land masses by d[illegible] [illegible]ists of [illegible] [illegible]nts

which

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Island. These plants failed to migrate on account of large barriers of deep ocean and remained confined to isolated regions.

Contrasted with the oceanic islands are the continental islands, which were once parts of the mainland and were separated from it in geologically recent times. These have few or no endemic species. Their flora and fauna differ but little from the adjacent mainland. The British Isles belong to this category.

Another fact of biogeography is that different regions that have similar conditions of the environment but are widely separated by long barriers of high mountains, large oceans or deserts are often inhabited by different species. Thus, the characteristic species of the American deserts are the cacti and those of the African desert *Euphorbias*. The basin of the Amazon in South America, the Congo Basin in Africa, and the south-eastern Asia, all have a tropical rain forest climate, but the plant and animal species of these rain forests are different.

EVIDENCE FROM COMPARATIVE ANATOMY

A strong support for the doctrine of evolution comes from the study of comparative morphology and anatomy. The fundamental similarity of cells and tissues that make up the bodies of plants (and animals) of very different groups indicates relationship. All the ferns are closely related to one another on account of similarity of their stelar systems, reproductive structures and life cycles. Similarly, all the angiosperms show a close relationship but different degrees of relationships can be recognised : the pea, grams and beans are closely related because they have a similar floral structure, while the petunias, maize and sunflower are distantly related, though all are seed plants.

Among the animals also, if organs or organ systems are studied in any large group, one is impressed by the great similarity throughout the group which shows that the structures in question are built on the same general plan. A few examples are described below.

Among the vertebrates, from the frog to man, the vertebral column is constructed on the same basic plan. The digestive system in the various classes of vertebrates is made up of corresponding organs which occur in the same order with the same kinds of secretory glands pouring their secretions at corresponding points in the digestive tract. Even muscles are arranged in the same manner; the large blood vessels follow the same general course giving off branches at essentially corresponding points and connected to the same organs.

Again, a great similarity is discernible in the brain of all vertebrates. The eyes and ears in the different classes of vertebrates are constructed on the same general plan, with the same parts arranged in the same order.

An important aspect of comparative anatomy is the occurrence

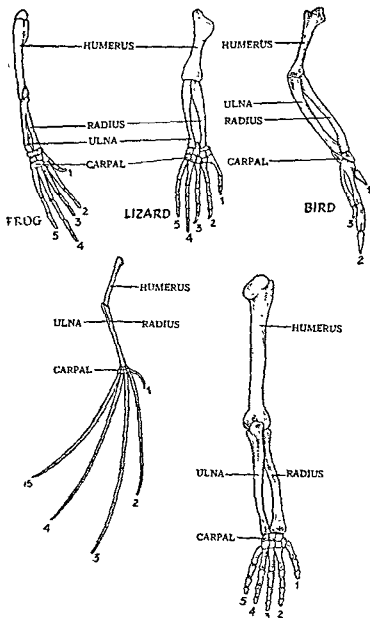


Fig. 15 1. The fore limbs of several vertebrates, showing the arrangement of homologous bones in the superficially different organs

of organs or body parts which have the same fundamental structures but may differ in appearance because they are adapted to serve different purposes. Such structures are said to be homologous. The fore limbs of several species of vertebrates such as amphibians (frog), lizards, bat, bird, horse and man are all constructed on the same pattern, and include the same bones in the same position (Fig. 15.1). *Why should similar bones have been created in the* formation of the wing and leg of a bat, used as they are for such totally different purposes ? The reason, why different organisms possess homologous structures, is that they are descended from common ancestors. They have become different in the course of evolution as a result of modifications to suit different needs. Instances of homologies are numerous both in the animal and the plant kingdoms. Homologies do not prove but they do suggest evolution. They are readily explained if we assume that different organisms have evolved from common ancestors ; they do not make sense on any other ground. Dobzhansky has correctly assessed the opinion of "die-hard anti-evolutionists" who regard homology to mean "only that the Creator gratuitously chose to make homologous organs in quite unrelated organisms." "This opinion", he says, "may be said to be implicitly blasphemous ; it actually accuses the Creator of arranging things so that they suggest evolution merely to mislead honest students of His works."

Sometimes, different structures look quite similar because they perform the same functions. Such structures are called analogous. Thus, the leaf-like structures of *Ruscus* and the needle-like 'leaves' of *Asparagus* are not leaf-structures but stem branches although they look like and perform the function of leaves. Similarly, tendrils of vine and pea are morphologically different structures, the former being of stem nature and the latter of leaf nature The wings of a bat, bird and butterfly are similar in function but differ greatly in organisation. The resemblance is due to analogy. Such resemblances are only superficial and the result of adaptation to more or less similar conditions of the environment. They do not indicate relationships

Analogous structures have different origins, but in the case of homologous structures the origin is the same. The latter indicate common ancestry. The greater the resemblance, the closer is the common ancestry ; the less the similarity, the more remote is the kinship. The resemblances, however, are not without significance. If there were no evolution, all organisms descended from the same ancestors should still be alike. The differentiation into species,

genera, and families would not exist. Since these differences do exist along with similarities, change must have occurred somewhere along the lines of descent.

EVIDENCE FROM VESTIGIAL ORGANS

Sometimes parts that are well-developed and are functional in many plants and animals are very much reduced structurally and useless functionally in other related plants and animals. Such reduced structures are called **vestigial**. In some compositae, the ray florets have an abortive pistil. This rudimentary pistil has no stigma and, therefore, cannot be fertilised. The ovules are also abortive. Similar abortive pistillodes occur in the male flowers of some cucurbiteceae and abortive stamens occur in some labiatae.

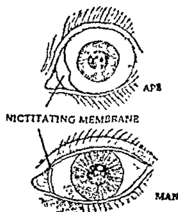


Fig. 15.2. Nictitating membranes in the eyes of ape and man (After Reles and Brown)

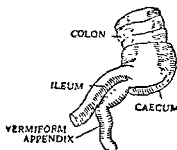


Fig 15.3. Vermiform appendix in man

There are numerous examples of vestigial organs in the animal kingdom. Most of the vertebrates (the birds, reptiles and amphibians) have a third eyelid which can be moved across the eyeball to cleanse it. But in man and other mammals it is represented only by an immovable fold, the nictitating membrane, at the inner corner of each eye (Fig. 15.2). Most mammals can move their outer ears. Muscles which are responsible for these movements are also present in man, but they have lost their power of moving the ear and have become vestigial. The presence of vermiform appendix in man is another example of vestigial organs. It is a blind tube associated with the alimentary canal. It serves no useful purpose here and even if it is removed it will make no difference to man. It is sometimes a nuisance because it is associated with the disease

appendicitis. The majority of mammals have a well-developed tail, *but in the* higher primates, to which class man also belongs, it is lacking. The rudiments of the tail are, however, *present in these* animals internally, in the form of a few caudal vertebrae although no sign of it is usually visible externally. Even the muscles, which in other mammals move the tail, are present in all of the primates. The birth of a girl with a three inch tail, in South India in July 1970, lends support to this view.

Many more examples of vestigial organs may be cited. The splint bones of horse are the remnants of lost toes. Snakes are without limbs and girdles, but the python possesses a remnant of a pelvic girdle and tiny useless hind limbs enclosed within its body. Kiwi is a bird that does not fly but feathers in reduced form are present. The existence of vestigial structures can be explained easily on the theory of descent with modification, rather it implies evolution. The vestigial structures had their day of usefulness and now linger on as relics of past history. In fact, their occurrence might have been anticipated. When a structure has outlived its usefulness, it is reasonable that it will persist in a much reduced form. The presence of a vestigial tail in man is a proof that our ancestors had a waggable tail. The persistence of appendix in man is similarly explained (Fig. 15.3). No other theory can adequately explain its presence. After all, why should a useless and disease-ridden structure have been created only to plague man? If plants and animals had been specially created they should have been created in perfect form.

EVIDENCE FROM COMPARATIVE EMBRYOLOGY

All sexually reproducing organisms begin life as one-celled zygotes. The study of the development of a new individual from the zygote by a process of cell division till the embryonic stage is called embryology. The study of comparative embryology in plants and animals offers another evidence in favour of evolution. *In some* plants, the juvenile forms are different from the adults. In *Pinus*, *e.g.*, the leaves on the seedling are borne singly on the stem in a spiral manner contrasting with the clustered arrangement in spurs on the adult plant ; the adult *Acacia* tree is characterised by highly compound leaves, yet its seedlings have simple leaves. It was thought that these characters belonged to some *ancestral forms* which were being repeated by the plants in their early stages of development. Similar observations in the animal kingdom led Haeckel

to put forward the **biogenetic law** according to which the embryos in their development repeat the evolutionary history of their ancestors in an abbreviated form. In other words, the different stages in the development of an individual (ontogeny) represent the different stages through which the race passed(phylogeny)in the process of evolution. This is expressed by the pithy statement that "ontogeny recapitulates (repeats) phylogeny." The single-celled zygote thus corresponds to unicellular ancestors and the early multicellular stage of the embryo of higher plants and animals corresponds to some colonial ancestors like *Eudorina* and *Volvox*.

One stage in the life history of a moss plant is the filamentous protonema which, according to the biogenetic law, indicates algal ancestry of the mosses. In their early stages of development, many animals show characters that resemble the characters of their ancestors. Thus, in the development of frog a tadpole larva is formed. The tadpole is very much like a fish It swims and breathes like a fish. This means that frogs have been evolved from fish-like

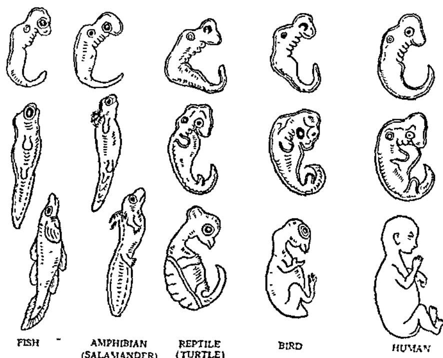


Fig. 15 4 Development of the embryo in vertebrates. Early stages of the development of embryos in different vertebrates as given in the top row show close resemblance. All of them have long tails and gill slits. The difference becomes apparent as development proceeds

ancestors. The appearance of gill slits in the mammalian embryos is interpreted as indicating fish-like ancestry for the mammals. Three distinct types of kidneys occur among the vertebrates. The simplest type is the pronephric kidney which is the only type that occurs in the most primitive vertebrates like the hag-fishes. In the adult fishes and amphibians, the pronephros is soon replaced by the mesonephros which is their functional kidney. In the higher vertebrates, the reptiles, birds and mammals, the two kinds of kidneys described above are formed one after the other but they are only temporary arrangement. Soon, a third type of kidney, the metanephros, is formed and serves as the functional kidney of the adult organism.

Now, why pronephros and mesonephros, which are characteristic of the lower vertebrates, be first formed and then replaced by the metanephros in the higher vertebrates ? This can only be explained on the assumption that the higher vertebrates are the descendants of the lower ones.

A reference to figure 15.4 will show that the young embryos of different vertebrates show a great resemblance to one another. All, including man, possess long tails and gill slits. In the early stage it is not easy, for example, to distinguish a human embryo from that of an amphibian.

The *recapitulation theory* as *originally* put forward has been severely criticised. It presumed that the various stages of the embryo of an advanced animal resembled the adult stages of its ancestors. Thus, all that would be necessary to trace the evolution of any modern animal is to study its embryology and the various steps in its evolution would unfold themselves in the succesive stages of embryo. This concept is fundamentally wrong and has been discredited. The embryo of a higher animal resembles primarily the embryo of a lower animal rather than the adult form of the latter. The occurence of slits in man's embryo does not mean that the embryo is in the fish stage but that this structure is homologous to the gill slits of fishes, reptiles and other mammals and may be intrepreted as evidence of affinity or as indicating general evolutionary trends. Such features are to be considered as retention or persistence of ancestral characters rather than recapitulation.

Such retentions of ancestral features frequently offer clues to the phylogeny of the organisms concerned. And there is a reason for this. When characters that belonged to the ancestors reappear in the descendants, it is because the genes that controlled their appearance in the ancestors have been transmitted to the offspring. The

repetition is, therefore, an evidence of an affinity that exists between ancestor and descendant.

EVIDENCE FROM COMPARATIVE PHYSIOLOGY

The study of comparative physiology and biochemistry in animals also provides ample evidence for evolution. Not only are the organs of digestion in the vertebrate animals similar in structure and location but they also show much similarity of functions. The enzymes that they produce are in the main similar. The parts of the central nervous system perform, so far as they have been tested, approximately the same functions. The chemical reactions involved in the process of respiration are essentially similar in most diverse organisms. Most animals can readily oxidise uric acid to allantoin which is more soluble and is eliminated from the body along with urine ; man is unable to do so and as a result, is liable to gout. In this inability, man resembles the tail-less apes.

Again, the blood sera tests give a remarkable proof of kinship. Animals, which on other grounds are very closely related, have been found to possess similar bloods. Thus, it has been experimentally proved that the blood of a horse and ass is similar, so is that of rabbit and hare, of man and anthropoid apes (chimpanzee *e g.*).

EVIDENCE FROM DOMESTICATION AND GENETICS

The evidences of evolution described in the preceding pages are indirect and of circumstantial type. Evolution is inferred from them as a logical deduction rather than a phenomenon which can be observed In fact, when Darwin put forward his theory of evolution in his "Origin of Species" on the basis of an enormous mass of observed facts, neither he nor any one else had seen a species changing into another. All that could be said was that the innumerable biological facts, which would otherwise fail to make any sense, could readily be explained on the hypothesis of evolution.

More direct evidence of evolution comes from the domestication of plants and animals and from the more recent study of genetics. Plants have been cultivated and animals domesticated by man since prehistoric times. Breeders have produced new varieties of plants and animals to suit their needs or fancies through the process of hybridisation of diverse varieties or races combined with artificial selection. The longer a species has been domesticated, the more numerous and diversified are its domesticated breeds. The pigeon

which has been domesticated since prehistoric times has 140 varieties, all descended from the wild rock pigeon : the dog which is perhaps the most ancient of the domesticated animals, having been brought under domestication about 10,000 years ago, has 200 varieties and the horse, first domesticated 3,000 to 4,000 years back, has 60 varieties.

The production of new varieties or races by breeding and selection involves considerable genetic changes. We will illustrate the effect of domestication with reference to horse in the animal kingdom and cotton in the plant kingdom. The modern domestic horse (*Equus caballus*) is descended from the wild horse that lived in the deserts of western Mongolia and which has been named *Equus przevalskii*. The wild horse in its history underwent many changes because its descendants were used for different purposes at different times, each purpose being served by a different genotype in the horse population. Natural and artificial selection perpetuated the suitable genotypes and eliminated the unsuitable ones. The result is the existing diversity of horse breeds.

The inhabitants of Mongolia and Middle Asia used the horse as a meat and milk animal, as well as for riding and carrying of personal effects. These horses had no speed. Then came the heavy and powerful type of horses of western Europe which the heavily armour-clad knights of the middle ages rode for warfare. When the warriors' armour was replaced by firearms, there appeared the draft horses and the farm horses which were used for the transport of heavy loads. They were tall and heavy. Then came the cavarly horses of the Greeks and Romans. Gradually, with the introduction of the saddles fitted with stirrups, there appeared several breeds of light-footed cavalry horses which were selected for their speed, agility and alertness. Among these were the famous breeds of Arabian horses. The thoroughbred race-horses were produced by hybridising these Arabian horses with the heavy horses of western Europe. The thoroughbred horse is known for its racing qualities and is quite different from its Arabian ancestors or from the wild Mongolian horse, which is its more remote ancestor. The evolution of horse nicely illustrates the great and controlled change which can be wrought by man in an animal by hybridising and selection.

Another example of the changes brought about by domestication is afforded by the cultivated cotton. Cotton was cultivated in the Indus valley about 4,000 years ago as evidenced by the fine fabrics discovered in the Mohen-jo-Daro excavations. It was also cultivated

by the American tribes long before the days of Columbus. The Indian cottons have 26 chromosomes (diploid number) in their cells, whereas the American cultivated cottons have twice as many chromosomes (52); hence the American cottons are tetraploids. Besides, there are some wild cotton species in America and the neighbouring islands which have 26 chromosomes. Cytological investigations, the details of which need not be given here, indicate that the tetraploid American cottons originated somewhat in the following manner. At some time in the past, somehow, an American wild cotton (26 chromosomes) crossed with an old-world cotton species (26 chromosomes). The F_1 hybrid contained 26 chromosomes, 13 from the American parent and 13 from the old-world parent. The two sets were, however, not similar and did not synapse. Then, somehow, a duplication of the chromosome complement in the F_1 hybrid occurred resulting in 52 chromosomes. Synapsis is now possible because each chromosome has its duplicate with which it can pair. As this polyploid contains chromosome complements of two different species, it is an allopolyploid. Thus, hybridisation between two different species followed by polyploidy (tetraploidy in this instance) and selection is responsible for the production of new species (*see* chapter 10).

Gene mutations have been referred to in an earlier chapter. As a result of mutation, the trait determined is different from the original. Gene mutations have been found to be fairly widespread in nature and can also be induced artificially. These form the basis of hereditary variability which is the raw material of evolution. More will be said about this subject in a later chapter.

An interesting aspect of gene mutations is the occurrence of **parallel mutations**. Sometimes, the same or similar mutations occur in related species of organisms. For example, the *RH* blood factor in man was so named because it was first discovered in Rheus monkey. This indicates the occurrence of homologous genes in man and the Rheus monkey and is a proof of their relationship.

Anti-evolutionists may still object to the above direct evidence on the ground that the changes brought about by domestication, polyploidy, mutation, etc. are small and do not change the species. The modern race-horse is still a horse. A fox-terrier belongs to the same species as a hound, and a mutant rose is still a rose and belongs to the same species as its ancestors. But this cannot be said of *Raphanobrassica*, a new species produced experimentally by Karpechenko in 1926 by crossing cabbage (*Brassica oleracea*) and

radish (*Raphanus sativus*). Both these plants have 18 chromosomes. The F_1 hybrid also has 18 chromosomes, 9 from cabbage and 9 from radish. The cabbage and radish chromosomes fail to synapse and the hybrid is sterile. Karpechenko's cabbage×radish hybrid, however, was not completely sterile. It produced some seeds which grew into F_1 plants. These proved to be tetraploids; they had 36 chromosomes in their cells, 18 chromosomes of cabbage and 18 of raidsh. The tetraploid hybrids were tall and vigorous plants.

Karpechenko had crossed cabbage and radish with the hope of producing a plant which combined the top of cabbage and root of raidsh. Unfortunately the hybrid had roots like the cabbage and foliage like the radish. The plant is a new species called *Raphanobrassica* and is important from the evolutionary point of view because it was the first new species (or genus) produced in experiment. It is fertile and breeds true and is sterile to either of its parent. In short, it is a new species by any reasonable definition. Since the discovery of *Raphanobrassica,* several new species have been synthesised by allopolyploidy. What man has achieved on a small scale is accomplished by nature on a much larger scale. The cultivated American species of cotton probably arose in this way. Allopolyploidy was perhaps a very common method of species formation in plants.

QUESTIONS

1. What are vestigial organs? Give some examples. How do they prove evolution?
2. "Ontogeny repeats phylogeny". Discuss this statement.
3. Describe briefly the various evidences to prove evolution.
4. What is comparative embryology? What light does it throw on evolution?
5. What light does the study of modern genetics throw on the concept of evolution?

16

THEORIES OF EVOLUTION

WHILE the doctrine of evolution is now accepted by most people as a definitely proved fact there was till only recently no general agreement among biologists as to the method and causes of evolution *i.e.* how evolution has taken place. To explain these causes several theories have been put forward within the past century. Only within the last few decades the work of cytologists and geneticists has gradually unravelled some of the processes by which evolution seems to have been taking place in nature through the ages. As a result of these investigations, a fair amount of agreement among the majority of biologists has been arrived at as regards the broad principles of evolution, but much yet remains to be achieved. Before coming to the modern conception relating to the processes that have contributed to organic evolution it is necessary to trace the history of evolutionary thought since the beginning of the nineteenth century.

THEORY OF LAMARCK
(1744—1829)

Jean Baptiste de Lamarck was a great French naturalist and a pioneer evolutionist of the pre-Darwinian period. In his book "Philosophie Zoologique" he put forward an explanation of evolution based on the inheritance of acquired characters. An acquired character may be defined as a structural change in the body of an organism involving a deviation from the normal, induced in the life time of an individual by change in environment or in function (use or disuse of organs). According to Lamarck the change so produced persists after the factors inducing it have ceased to operate.

Briefly stated, the theory of Lamarck is as follows. Organisms live continuously in some kind of surroundings, so that environments

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ment and the effect of use and disuse of organs. But these factors are useless in evolution unless the third factor, i.e. the inheritance of acquired characters, is operative.

ARE ACQUIRED CHARACTERS INHERITED ?

The transmission of acquired characters is crucial to the theory of Lamarck.This question has engaged the attention of scientists from time to time and is also of interest to laymen who are often led to explain adaptive characters as due to the influence of the environment. Lamarck believed that characters acquired by the individual during its lifetime were transmitted to the offspring. Lamarck's hypothesis had no experimental basis. Geneticists are the persons who are most qualified to know about heredity. Their work has disproved Lamarck's views. Numerous experiments performed during the last one hundred years also give negative results. Many of the experimental observations put forward in support of Lamarckian inheritance have either been repudiated by other scientists who repeated those experiments or are capable of alternative explanations. Modern biologists have, therefore, abandoned the idea of inheritance of acquired characters.

But before dismissing this question let us study its pros and cons. Mice and sheep whose tails are cut generation after generation do not beget offspring with cut tails; dogs with trimmed ears never produce young ones having this mutilation. The battle scars on the bodies of war veterans do not reappear in their children and it is fortunate that it is not so, for otherwise the human race would soon come to consist of cripples. The skilled hand of an artist and the highly developed muscles of a wrestler are not inherited. They have to be acquired in each generation just as surely as learning to read and write.

Cases of congenital diseases are sometimes erroneously quoted as proofs of the transmission of acquired characters. Congenital syphilis or tuberculosis are the result of the infection of the embryo at some stage of its development by the germs present in the mother's body.

A good example of the failure of disuse to produce Lamarckian effect was provided by the work of Payne (1911) who could not detect any effect on the eyes or the phototropic responses of *Drosophila* after sixty-nine generations of disuse. The argument often put forward, that the inherited effects of function or evironmental

are always working on them. The effects of the environments are, however, not always obvious because it takes a long time before the results are manifest. Changes in the environments, as for example, resulting from migration, lead to changes in the needs and wants of the organisms, especially the animals. The changed needs are met by a change in the habit or activities of the animal. The new activities involve the greater use of certain organs which will meet the new requirements, and the disuse of certain other organs which are no longer needed in the new conditions. It is a well-known fact that continuous and extra use strengthens and develops an organ and disuse results in its degeneration and ultimate disappearance. Lamarck believed that variations thus produced are passed on to the next generation and are piled up generation after generation until they result in notable change in bodily form. Thus, new needs result in the development of new organs as a result of efforts put forth by the animal and the development of parts already existing accompanied by the disappearance of parts no longer needed. In the lower animals that are devoid of consciousness and in plants, variations are produced as a result of the direct effect of the environment.

Lamarck cited numerous examples to illustrate the effects of conscious effort on the part of the animals. The oft-quoted examples are those of the giraffe and the snake. The ancestors of the giraffe were forced to live in conditions where there was not enough grass and herbage to eat and they were obliged to browse upon the foliage of trees. The conscious stretching-up effort which the animals had to make to reach this food which grew progressively higher and higher resulted in the elongation of their forelegs and necks. The increase was cumulative from generation to generation.

The loss of limbs in snakes is the result of gliding and concealing habit. The lizard-like ancestors of snakes were limbed animals, but when mammals arose, these reptiles began to live in burrows so as to conceal themselves. The result was a gradual reduction and eventual loss of limbs which were not needed. The gliding movements in the earth, repeated generation after generation, made the body flexible. Similarly, birds like the duck, which did enough food on land, were forced to seek food in wat had to spread out their toes and stretch their le purposes. The result was the webbed feet and long

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modification are so slight that they cannot be detected experimentally but require cumulative action through thousands of generations to become obvious, is not deserving *of any attention. With the* advancement of scientific technique it is now possible to detect even the minutest difference.

A similar objection applies to mammalian teeth. The teeth of the animals are adapted to the type of food that they take. The only effect of use in these cases is *the wearing away of the biting and* grinding surfaces of the teeth as a result of mechanical abrasion.

Many cases of cryptic resemblance of animals to the prevailing colour of their habitats are often explained by Lamarckists, on the basis of the direct effect of the environment. There may exist, notably in insects, *some cases of modification, but most of these* characters have now been found to be of genetic origin and in many cases it seems reasonable to suppose that they evolved as a result of selection in their favour.

The greatest setback to Lamarckism was Weismann's theory (1892) of the continuity *of the germ-plasm, which may be briefly* stated as follows. The new individual develops as a result of the division of the zygote which is formed by the fusion of two sex cells or gametes; the whole inheritance of the individual must, therefore, be contained in the zygote. In the higher animals, for example, most of the cells which result from the division of the zygote become differentiated into the various parts and tissues of the body, some into muscles, others into bones, or nervous tissues. A few cells, however, remain undifferentiated. These later give rise to egg-cells or sperm-cells rather than to any part of the body proper. The cells which make up the body were called by Weismann the **soma**, whereas the cells which function in reproduction were called by him **germs** cells or collectively the **germ-plasm**. Now Weismann maintained *that the germ-cells carried over to the next generation.* In other words, the germ-plasm continued through successive generations, but the soma came to an end with the death of the body. As the new individual arises only from the germ cells, any modification that occurs in the soma (acquired characters) cannot be transmitted to the offspring as the soma is not concerned in reproduction. This is, in fact, what should be expected.

Weismann's views raised a hot controversy but most biologists finally accepted them as sound. *It is well-known that the child does not* inherit the scholarship of his parents, but only the capacity to learn. The child must begin his education, not where his

father left off, but at the alphabet, and he will not learn any faster because his farther was educated.

As evidence of the soundness of Weismann's theory we may cite an instructive experiment by Phillips and Castle. An albino female guinea pig was selected and before it attained sexual maturity, its ovaries were replaced by the ovaries of a young black female guinea pig, which had not yet reached maturity. When the grafted animal matured, it was mated with white male animal. Now it is a well established fact of genetics that, in the case of guinea pigs, a white × white mating always gives white offspring. It is, therefore, certain that if this female had not been operated upon she would have produced only white offspring as a result of the above mating. Actually, the offspring that she produced were all black. The transplanted ovaries of black guinea pig remained in the body of the white animal for several months without being influenced by the new environment. In other words, heredity is determined by the germ-cells and not by body cells.

Bonnier studied the effect of transferring plants from the plains to the alpine regions. The new environment produced considerable changes in the phenotype and in some cases the change was so great that it almost resembled another species in the plains. When, after 18 years, the plants were transferred back to the plains, they lost their alpine characters and returned to their original characters. This shows that even a long period of acclimatisation to the new environment had not affected the breeding behaviour of the species.

Last of all, the mechanism of heredity as revealed by modern genetics makes inheritance of acquired characters highly improbable. Hereditary traits are determined by the genes which are transmitted to the next generation through the sex cells. The body cells take no part in this transmission. Thus, exposure to sun may cause the production of colour in the skin but this will not influence the genes in the sex cells, which alone will determine the skin colour in the next generation.

Before closing this subject we may describe some experiments cited by neo-Lamarckians in an attempt to revive the question of inheritance of acquired characters. McDougal dropped rats in a tank of water which the rats could leave by two landing places after swimming. One of the landing places was lighted but electrified so that the rats landing on it received a shock ; the other was dark and shock-free. The landing places were constantly changed. The rats had to learn to use the dark shock-free landing place. The

number of trials that were necessary before the rats learnt this lesson progressively decreased in successive generations ; it was 100 in the first generation and 25 in the twenty-third generation. Evidently, the training received by each generation was passed on to the next generation and its effect was cumulative. McDougal's experiments were repeated by Crew but *his results entirely contradicted* McDougal's Lamarckian claim. The discrepancy has been ascribed to lack of control and inadequate attention to genetic control on McDougal's part. It appears that McDougal unconsciously selected strains of rats whose genotypes endowed them with favourable reaction to training.

Kammerer worked on *Salamandra atra*, a black highland species which normally produces two young ones at a time. When this species was subjected to moist and warmer conditions, it could be induced to produce more young ones (up to six) which took to water like *S maculosa*. Similarly, *S. maculosa* which normally produces numerous young ones which live for six months in water, when exposed to terrestrial and alpine conditions, produced only two or three young ones which were terrestrial having only vestigial gills. Unfortunately, these results have not been confirmed by other investigators.

The discovery of hormones and their influence has provided the *supporters of neo-Lamarckism with a strong argument against* Weismann's objection. The sex hormones produced in the sex glands are carried to the rest of the body through the blood-stream and have a remarkable influence on secondary sexual characters, such as the growth of hair and breaking of voice in man and the development of breasts in woman. It is contended that the external influences which modify any part of the body may influence the secretions produced by the modified part and these may reach and affect the germ cells.

A somewhat similar explanation of the mechanism of the inheritance of acquired characters was put forward earlier by Darwin *(1868) in* his "provisional hypothesis of pangenesis". He supposed that all organs gave off particular kinds of particles,called gemmules or pangenes. These are carried through the blood stream to the sex glands where they accumulate and multiply as the germ cells develop. Every part of the body is thus represented in germ cells by a gemmule. Body cells modified by the environment might so modify the gemmules that the modification will reappear in the next generation. This theory has long been discarded. Even the inheritance

of acquired characters which it proposed to explain, stands discredited in the eyes of most biologists. We have dealt with this subject at a greater length than it deserved on account of popular belief in it.

DARWIN'S THEORY OF NATURAL SELECTION

A theory that has exercised the greatest influence on evolutionary thought was the theory of natural selection put forward by Charles Darwin in his book "Origin of Species" in 1859. Darwin supported his theory by a great wealth of observation relating both to the plant and the animal kingdoms which he had collected over a period of several years. Almost similar conclusions had been reached at the same time by another naturalist, Alfred Russel Wallace. The main points of Darwin's theory are described below.

1. **Overproduction.** All plants and animals tend to multiply at a high geometrical rate. A plant of shepherd's purse produces nearly 40,000 seeds and the evening primrose more than 118,000 seeds. If all the offspring of any species should survive and then reproduce, a single species would occupy all the available space on this earth in a few generations. Some plants are even more prodigal than the plants mentioned above with respect to reproduction. The number of spores produced by a single fern plant or a mushroom often runs into millions. The reproductive capacity of bacteria is well known. Under favourable conditions, a bacterial cell may divide and produce two individuals after every 30 minutes. If this process continued uninterrupted and all the offspring survived and reproduced again, the number of descendants produced by a single bacterium in 24 hours would run into billions.

A single salmon produces 28,000,000 eggs in a season and a starfish produces about a million eggs in a year. Assuming that there is 100 per cent survival, half of these eggs would mature into females, each of which would again produce an enormous number of eggs. It is obvious that, if such rates of reproduction were to continue even for a few generations, soon a single species of fish would fill all the seas and be eventually pushed out onto the land by the mere pressure of reproduction.

Essentially the same principle applies in the case of even the solwest breeders. Elephant is perhaps the most slowly breeding of animal. Its average life span is of about 100 years, with an active breeding period of sixty years. During this period, a single female will produce about six offspring. If all these survived to their full

length of life and *reproduced at the same rate*, the number of descendants of a single pair after only 750 years would be to the tune of about 19,000,000.

It is thus clear that, as a result of the *geometrical rate* of increase even in the slowest breeding species, its number would soon become much larger than can be supported on this earth. This, however, does not happen because usually the number of offspring that reach maturity and reproduce is just enough to maintain the species.

2. Struggle for existence. The reason for the great disparity between the numbers produced and those that survive to the reproductive stage is the large-scale destruction of the new offspring, especially in their young stage. This is due to the ceaseless struggle that goes on among the descendants of plants and animals. The space and food available being limited and not enough to sustain all the organisms brought forth by reproduction, a struggle among *them for the necessities of life follows as a necessary corollary*. The struggle is a many-angled phenomenon ; it is for food and space and in the case of plants for light ; it is against the enemies and the predators that kill and destroy ; it is against the factors of the environment like extremes of heat and cold, and drought. This struggle is called the struggle for existence. It is most intense between individuals of the same species (intraspecific) because they compete for identical requirements of life and are exposed to similar dangers ; for the same reason, but to a lesser degree, the struggle is more acute between species of the same genus than between species belonging to different genera. In this ruthless struggle, death is the law and life an exception. The majority of participants perish or are destroyed before they reach maturity and are thus eliminated *without leaving any offspring ; only a comparatively much smaller* number comes out successful in this life-and-death struggle and reaches the stage of reproduction. These alone reproduce and leave offspring. The struggle for existence is the struggle for self-preservation and self-perpetuation. It is, in short, the struggle for survival which acts as an effective check on the tremendous increase in the population of each species which would otherwise occur.

3. Variations. The struggle for existence has its inevitable losers and winners. Now, what shall decide the result of this struggle ? Which ones would be exterminated, which survive ? According to Darwin, the outcome of the struggle would be determined by the qualities of the individuals. It is well known that individuals show

great variation and diversity of form amongst themselves. No two individuals of the same species are exactly alike. Except in the case of identical twins, no two offspring of the same parents are cast in the same mould. There are readily observable differences which enable one to tell one individual from the other. The variations are of three kinds, namely, of the neutral type, harmful and useful. The neutral variations give to the possessor neither any advantage nor any disadvantage in the struggle and are of no significance to the organism. Most of the variations within or between species, *e.g.* variations in leaf form, type of stem branching or size and shape of fruit, belong to this category. Some variations are definitely harmful and hinder and handicap the individual in the struggle. Even the slightest handicap will place the individual at a great disadvantage and result in its extermination. Thus, a plant with deficient chlorophyll in the leaves will fair badly on account of low vigour that accompanies lower rates of photosynthesis Other variations are such as give some definite advantage to the possessor over others and, therefore, increase its chances of survival. Thus, variations that tend to reduce water loss in desert plants, increase the resistance of a plant to frost, favour pollination or aid in seed dispersal have survival value and the plants that possess them are at an advantage over others in the matter of competition. Similarly, variations that increase the speed of an animal or improve its sensitivity of smell, hearing or sight will aid it in escaping predators and improve its chances of survival.

4. **Natural selection.** It will be evident that those individuals, that are possessed of profitable variations that are of advantage in relation to other organisms and conditions of life will succeed in the battle for life, will eventually survive. In other words, those that are best adapted to the natural conditions will survive. The struggle for existence thus leads to the survival of the fittest or death of the unfit or less fit.

The fittest in one generation or the favoured individuals alone reach maturity and reproduce and transmit their useful variations to their offspring among which variations again occur. In the struggle that ensues, some again survive and others perish ; the former in their turn pass on their profitable equipment to their offspring, and thus the process continues generation after generation. In this process, organisms with unfavourable variations will be eventually supplanted and will become extinct. The "survival of the fittest" is a type of selection exercised by nature in a quiet and imperceptible

way. Darwin called it **natural selection** to distinguish it from the **artificial selection**, as exercised by man in the improvement of his *cultivated plants and domestic animals*.

What man can achieve with a smaller number of individuals and in a much shorter time has been achieved by nature on an enormous scale, working as it does on an infinitely large and infinitely diverse population over a period of time which is counted in hundreds of millions of years.

Darwin's use of the superlative word "fittest" would mean that only one fittest survived and all the rest perished. The struggle for existence leading to natural selection is not so severe. It is simply the fit, rather than the fittest, who survive.

The expressions like "struggle" and "competition" should not be considered in the same sense in which they apply to human affairs. They are rather metaphorical. Thus, trees struggle against the danger of being felled by wind by developing stronger root systems ; mammals and birds struggle against cold by developing heat insulation, temperature regulation, or by remaining dormant during winter months ; desert plants struggle against dryness by having their leaves transformed into spines- and cutting down transpiration. Plants, and animals compete for food when food is scarce, but they do not necessarily fight against one another.

As to variations, Darwin considered that minute variations *of the fluctuating type were more important in evolution* than the discontinuous variations. These variations piled up generation after generation. It is the accumulations of these slight variations through several generations that give rise to more important modification of structure that ultimately lead to the development of new species out of old ones. Individual differences are the first step towards slight varieties ; these lead to more strongly marked and more permanent varieties ; these in turn lead to the formation of sub-species.

Darwin's theory of natural selection may be illustrated with reference to the famous case of giraffe. In any generation of giraffes the length of the necks will tend to vary ; the animals that have *slightly longer necks than their fellows will get the* best food ; these will tend to survive and, therefore, pass on their advantageous equipment to their offspring.

Variation is the material on which natural selection works and these variations must be inheritable. While variation *is a* progressive force in evolution that causes the production of modifications, heredity is a conservative force that tends to preserve these

modifications. Darwin knew nothing about heredity and was not clear as to the causes of variations. This was the weakest point in his theory and he was conscious of it. He thought that the two Lamarckian factors, direct action of environment and use and disuse of organs, were important in this respect. Among animals, the influence of habit was also considered as very strong.

MUTATION THEORY OF De Vries

The variations which Darwin considered important in evolution were of the minute fluctuating type or the continuous variations Large variations, which he called sports, were of no significance. Hugo de Vries, a Dutch botanist, put forward the theory that new races and species originate discontinuously and not gradually. Fluctuations, according to him, were dependent upon nutrition and did not result in any permanent change. Cultivation and improved nutrition, for example, result in minor differences in size, luxuriance and productivenesses in plants. Selection acting upon these fluctuations may change the average condition of the race, but such changes will persist only so long as the conditions which produced them are maintained. As soon as selection ceases, the race gradually returns to its former condition. A permanent racial change, according to De Vries, is not the product of a fluctuating variability but springs from a discontinuous variation or sport, which he called **mutation.** Mutations are sudden heritable changes which occur in organisms in unpredictable directions and which cannot be attributed to environmental effects or to cross-breeding De Vries thought that mutation involved a change in the nature of the germ cells, whereas fluctuation was an effect of the environment. The latter may modify the soma, and also the germ plasm temporarily, but not permanently. Permanent changes in the germ plasm, according to De Vries, arise spontaneously out of internal conditions and are not necessarily adaptive in nature. Most of them perish because they are not adaptive (*i e.*, beneficial) in character : only those mutations survive in a state of nature which chance to be adaptive. The environment does not cause mutations, but only determines which ones may survive. In the opinion of De Vries only large and discrete mutations were important in evolution and small mutations did not play any significant role. The new species appears all at once ; it originates from the parent species suddenly in a single step without any visible preparation and without any series of tran-

sitional forms. Evolution is thus primarily due to internal causes, but its course is guided by the environment, which selects those mutations which are capable of survival. Natural selection is still a factor but its action is restricted to the elimination of forms which are poorly adapted to the environment. As De Vries expresses it "natural selection may explain the survival of the fittest, but it cannot explain the arrival of the fittest."

De Vries based his theory on the experimental study of evening primrose (*Oenothera Lamarckiana*). This biennial plant is cultivated in Europe for its bright yellow flowers. De Vries found it growing in a wild state in a deserted potato field at Hilversum near Amsterdam in Holland in 1886 and was struck by its variability. During the course of several years, he observed over a dozen new types, some of which were new species. They were produced year after year from the seed of the parent species, and from their first origin bred true to their distinctive characters.

One of these mutants was characterised by the short style of its flowers (*brevistylis*) ; another by its dwarf habit (*nanella*) ; a third by its vigorous growth (*gigas*). The last named, often called the *giant*, was no taller than the parent species but was much stouter, with large leaves and flowers. It may be noted that in his experiments on *Oenothera Lamarckiana*, De Vries observed that the same mutations occurred repeatedly year after year in pedigree cultures from self-fertilised plants. Most of these mutants were constant from the seed and never reverted to the original *O. Lamarckiana* type.

Later studies showed that the mutations observed by De Vries were of complex types. Some were produced by changes in single genes and others were due to changes in whole chromosomes In *O. Lamarckiana*, the diploid chromosome number is 14. *O. gigas* is a tetraploid form with 28 chromosomes and another form was a triosomic with an extra chromosome in its nucleus ($2N=15$ or $14+1$).

QUESTIONS

1. Write an essay on the inheritance of acquired characters.
2. Give a brief account of Darwin's theory of natural selection.
3. Describe briefly the mutation theory of De Vries.
4. Explain Weismann's theory of 'continuity of the germplasm.'

17

MODERN SYNTHESIS IN EVOLUTION

HISTORICAL

In the last chapter we have outlined briefly the history of evolutionary thought in the nineteenth century. Darwin's book "Origin of Species" published in 1859 was widely read and one result of it was that the idea of evolution was firmly established. His theory of natural selection also found wide acceptance. While there were critics of the theory, they were outnumbered by the supporters of Darwinism among whom were some of the leading biologists of the nineteenth century, notably T.H. Huxley, Herbert Spencer and George Romanes in England, David Starr in Jordan, Asa Gray in the United States, and Carl Gegenbaur, Ernst Heckel and August Weismann in Germany. In spite of the opposition of the church in Europe, there was a general and widespread belief in the Darwinian concept of "descent with modification" in which "natural selection" played a leading role The arguments contained in Darwin's book and added to by his enthusiastic supporters seemed convincing.

But this rapid success of Darwinism met with a setback which began in the closing years of the last century and became more accentuated with the dawn of the present century. The first step in this direction was William Bateson's book, "Materials for the study of Variation" published in 1894. The author presented a large and impressive collection of evidence of variation which was discontinuous, as opposed to the continuous variation postulated by Darwin. This paved the way for the mutation theory put forward a few years later (1901, 1905) by De Vries. It was contended that the raw material for evolution was provided not by the minute continuous variation but by large mutations which also determined in a great measure the course of evolution. Selection was relegated to a wholly secondary position.

The rediscovery of Mendel's laws in 1900 dealt another blow to Darwinism. Mendelism then dealt with clear cut and large differences, and it was naturally supposed that hereditary factors only produced effects which were sharp and discontinuous and that the continuous variation which is obviously widespread in nature is not heritable. The gene theory put forward later by Morgan proved a big stumbling block in the way of Darwinism. The gene was then regarded as permanent and unchangeable. This being so, heritable variations could not arise. Genetics and cytology thus appeared to contradict the facts of palaeontology.

Johannsen's work on the inheritance of size in beans also seemed to minimise the role of selection. He showed that in genetically pure lines selection is without any effect. Coupled with the mutation theory of De Vries, evolution was now conceived as a series of mutations in pure lines. Natural selection found small place or none. Darwinism thus lost much of its prestige ; about fifty years back it was more or less dead.

Then, about the year 1927, a reorientation in the views of biologists took place. With the discovery of mutation in the genes and chromosomes it was realised that Mendelism could be reconciled to Darwinism.The gene was no longer regarded as permanent. It was subject to change. Changes in the genes resulted in the production of variations in characters. The gene thus came to be regarded not only as a unit of development and heredity but also the unit of mutation (or variation). The physical basis of heredity is also necessarily the physical basis of evolution.

Mutation could be large or small. Experimental genetics showed that small mutations were more important in evolution, the large ones being mostly fatal. These small mutations arose as a result of a discontinuous process. This reconciles the difference between the conception of Darwin and that of De Vries. Modern Mendelism thus has removed the greatest difficulty of Darwinism relating to the origin of heritable variations. Thus, one important result of the advances in cytology and genetics has been the rebirth of Darwinism in a modified form. This is designated as **neo-Darwinism**, since it is the outcome of facts which were unknown to Darwin. In this new synthesis, natural selection plays a directive role and explains the progressive role of evolution. Neither mutation nor selection alone is creative of anything important in evolution ; but the two together are creative.

The modern idea of evolution thus combines the ideas of Mendel-

ian genetics, the phenomena of mutations, the concept of Darwin's natural selection, and the knowledge gained from cytology into one theory. These and several other branches of biology like ecology, taxonomy, embryology, morphology, biogeography, etc., all contribute to an understanding of the evolutionary problem. There is hardly a branch of biology that does not make some important contribution to the study of evolution. This is the modern synthesis and is one of the basic and most important generalisations of the biological sciences.

ORIGIN OF VARIATION

A characteristic and important feature of all living things is heredity by which "likes beget likes". Heredity is a conservative force. However, if children were to be exact copies of their parents, evolution could not occur. Heredity is accompanied by an opposing force—the process of change which we call variability.

The main problem of evolution is the manner of origin of heritable variations. Lamarck was the first biologist to attempt an explanation in this field, but his theory of the effect of use and disuse and the inheritance of acquired characters has long been abandoned because experimental evidence was mostly against it. Darwin bypassed the problem. He thought that all variations were inherited and left the matter at that.

Within the last forty years, great developments have occurred in the fields of cytology and genetics. It is now recognised that self-reproduction occasionally results in imperfect or altered copy of the parent, called a mutant. Heredity and variation go side by side. The units of heredity and of mutation are the same, *viz.* bodies of molecular dimensions called genes. In the last analysis evolution is a sequence of changes in the genes. Mutations produce changes and heredity preserves these changes by their faithful self-reproduction until they are further altered by new mutations. The various types of mutations that have provided the raw material for evolution are gene mutations, chromosomal mutations and polyploidy. These have already been described in chapter 10.

1. The role of gene mutations in evolution. It is now generally agreed that gene mutations have played a major, though not exclusive, role in evolution. They provide the bulk of hereditary variations which furnish the raw material on which natural

selection operates. The gene mutations may be harmful, neutral or definitely advantageous. The useless or the less useful ones are gradually eliminated by natural selection on account of higher rate of mortality among them. Natural selection thus acts as a sieve that preserves the useful mutations. The larger and abrupt variations of the type considered important by De Vries are mostly harmful or more often lethal and are, therefore, useless in evolution. Small mutations, with slight effects, many of them often affecting the same character, are much more important in evolution. The organisms that possess useful small variations have better chances of survival and leaving progeny. These slight variations pile up generation after generation and ultimately become large enough. This is essentially the principle of Darwinism in a modified form.

The question might well be asked why most of the mutations are useless and why at all should they be produced? The answer to the first part of the question has been given in chapter 10. In answer to the second part of the question it may be said that the uselessness or usefulness of any mutation is not absolute. A variation that is useless in one environment may be useful in another and *vice versa*. A species that normally lives in a particular environment has become adapted to that environment as a result of a long series of mutations. If the environment changes, the adaptedness of the species due to old genes is disturbed and can be restored only as a result of genotypic reconstruction brought about by some chance mutation which may restore harmony between the species and the changed environment. Some mutations just happen to be useful in the new environment and in combination with new components of species genotypes. The mutant genes which might have been useless, or even harmful under the old environment may then become normal under the new conditions and replace the genes that were normal in the old environment. The old genes may reappear from time to time by mutation. They will now be harmful and will be eliminated. A species that is comparatively stable and does not show mutations will be at a disadvantage under the changed conditions. Moreover, it may be emphasised again that all mutations occur at random. They do not occur in response to any need of the organism or as a result of the effect of the environment. Adaptations to xeric conditions, for example, have not come about because plants foresaw the need for morphological and physiological peculiarities of

survival value ; they have survived because of some random mutations that are by chance adapted to these special conditions of life.

Single mutations play some role in evolution, but are not so important by themselves. It was stated in an earlier chapter that a gene often influences several characters and a single character is often the result of the action of many genes situated at different loci. Moreover, the genes interact with one another in the production of their effects. What the effects of a gene would be is determined to a very great extent by the other genes present in the organism. Thus, a gene **A** may be neutral in combination with another gene **B**, harmful with a gene **C**, but useful with a gene **D**. Thus, the value of a mutation depends upon the genes with which it becomes associated. Natural selection acts upon these gene combinations, preserving those that increase the adaptedness of species.

This theory seems plausible in every respect It takes into account the Darwinian principles of overproduction, struggle for existence, variation and natural selection. But the fluctuating variations of Darwin have given place to small mutations. This theory is known as neo-Darwinism on account of the emphasis that it places upon natural selection. It is supported by a huge mass of research in genetics, cytology and biochemistry, and claims wide acceptance among biologists.

It was stated earlier that gene mutations provide the bulk of evolutionary material. Gene mutation is, however, not the only method by which heritable variations have arisen. A part of the raw material for evolution has also been provided by chromosomal rearrangements and changes in the chromosome numbers.

2. The role of chromosomal rearrangements in evolution. The different types of chromosomal rearrangements, namely deficiency and deletions, duplications, reciprocal translocations and inversions, have been described in chapter 10. These result in alterations in the number or sequence of genes without causing any change in the total number of chromosomes. Deficiencies and deletions do not seem to have played any significant role in evolution as they are often harmful or lethal.

The effects of duplications on development are less deleterious than those of deficiencies, so that relatively long duplications survive. Duplications are of importance both to the individual and the race. Their immediate effect is to produce abnormalities in bodily characters. This is but to be expected, since they alter the genic balance.

In a zygote formed by the union of a normal gamete with one carrying a duplication (or repeat) there will be three doses of certain genes as compared to two doses of the rest. A large dose of certain genes may push to extreme form some of the traits determined by them.

Duplications are of much greater importance in evolution. Evolution has proceeded from simple to more complex forms. This has, doubtless, *been accompanied by a progressive increase in the* number of genes in a cell. Now, genes can be produced only from pre-existing genes. Duplications constitute the chief method (the other is polyploidy) by which the number of genes in a germ plasm is increased. This process and the repetition of it in evolutionary history is responsible for providing duplicate and multiple factors. Moreover, the duplicated genes offer greater material on which mutation can act, thus providing greater differentiation in nature. In the beginning, the repeated genes are merely copies of each other, but in evolution they may become different as a result of divergent and repeated mutations Duplications, thus, become a source of new genes in evolution.

Translocations and inversions are sometimes responsible for varietal differences in many plant species and play some part in species differentiation. Sometimes the effect of these phenomena, which has been described as 'position effect' is equivalent to a gene mutation.

According to the mutation theory to which most geneticists now subscribe, genes are independent units which are arranged on a chromosome in a fortuitous linear order and evolutionary modifications have arisen as a result of changes in their nature and properties (mutations in the strict sense). But the discovery of the position effects would seem to show that the action of the genes is dependent upon their neighbours and a gene occupies a particular *position on a chromosome because it acts well in that position*. The coordinations of action is not only between adjacent genes but the influence of a particular gene extends much farther; it may go as far as a dozen bands in the salivary-gland chromosomes. *A chromosome* is not just a container for independent genes but a hormonious system of interacting genes. Any change in this system as a result of chromosomal rearrangements *leads to mutational effects*. Such a change is known as **systemic mutation** in contrast to gene mutation by which is meant a substantive change in the nature of the gene. As *an alternative to the theory of gene mutations*, Gold-

schmidt holds that systemic mutations constitute the actual genetic basis for the separation of species.

The arguments put forward by Goldschmidt are too complicated and beyond the scope of this book, but a few points may be noted here. A large number of phenotypic changes in *Drosophila* which were previously regarded as due to gene mutations have now been found to be position effects. This discovery has been possible because the giant sized salivary gland chromosomes of *Drosophila* make the study of chromosomal rearrangements possible. It is probable that many of the so-called gene mutations in other species also are the result of similar changes in the gene pattern of the chromosomes although this correlation is not actually seen, because in their case the salivary gland-chromosome technique is not available.

Dobzhansky has made a detailed study of the chromosomal differences between several allied species of *Drosophila*. He has worked out their phylogeny and has come to the conclusion that they are related amongst themselves by different degrees of chromosomal inversions. In other words, the mechanism which has caused their differentiation is to be looked for in chromosomal rearrangements.

Makino's chromosomal study of the Japanese fishes, *Misgaurnus anguillicaudatus* and *Barbatula oreas* is also instructive. The former has an haploid chromosome number 26, and the latter 24. Most of these chromosomes are rod-shaped. In *B. oreas*, however, two chromosomes are V-shaped. Makino's conclusion seems reasonable that the reduction in the chromosome number has been accomplished by translocation, thus uniting originally distinct chromosome pairs.

Similarly, in *Drosophila*, the haploid chromosome number in different species varies from three to six. *D. palustris* has six chromosomes, all rod-shaped and one-armed ; *D. texana* has five, of which four are one-armed and one is two-armed. It appears that in *D. texana* two of the *Palustris* chromosomes have combined into one. Similarly, the smaller numbers of chromosomes in other species appear to have been derived from the larger numbers by different manners of combination.

A somewhat similar situation obtains in *Datura*, in which more than forty so-called "prime types" occur. These differ from each other merely by segmental rearrangements of chromosomes, which appear to owe their origin to reciprocal translocations. These prime

types show no visible differences, but they *occupy different* geographical regions. Presumably, mutation and selection would lead to visible *differences between the various* chromosomal types.

It would thus appear that the significance of chromosomal rearrangements lies in their providing a special method of species formation Goldschmidt, however, regards them as of greater importance in evolution than the true gene mutations which according to him are in reality only the effects of small chromosomal rearrangements. However, it has been demonstrated that there is a real distinction between the two types of mutations, since ultraviolet radiation can produce true gene mutation but not the chromosome breakage needed to effect sectional rearrangements, however small. 'This is," in the words of Huxley, "*prima facie* evidence that the substantive changes due to true gene mutation do (as is to be expected) play a part in nature, in addition to the *organisational* changes due to rearrangement of pre-existing units."

"From the point of view of evolution, however, the significance of such (systemic) changes will be very similar to that of true or substantive mutation; the changes produced will be inherited according to Mendelian laws, and will be of some extent." We may, *therefore*, conclude that the true gene mutations and the systemic mutations of Goldschmidt together constitute the most important source of *evolutionary change*.

According to Gustafsson, best results are obtained if gene mutations are accompanied by simultaneous sectional rearrangements. The latter provide a new internal environment for the new gene.

3. Role of polyploidy in species formation. Of the two types of polyploidy, allopolyploidy has been more important in evolution. Many of our cultivated plants are allopolyploids having origintated as a result of hybridisation followed by chromosomal doubling.

An important allopolyploid series is that of wheats. Wheats are of three kinds: Einkorn group with 14 chromosomes (*2N*; *AA*), Emmer group with 28 chromosomes (*4N*; *AABB*), and Vulgare group with 42 chromosomes (*6N*; *AABBDD*). The seriation at once suggests that the three types constitute a polyploid series with diploid, tetraploid and hexaploid numbers. The commercial American cottons are also *allotetraploids* (*4N*=*52*). The cultivated species of *Gossypium* in Asia and Africa are diploid plants (*2N*=*26*) and so are some American wild species of *Gossypium*. It is supposed that the cultivated American cottons arose as a result of natural crossing between some old-world species and American wild species

of cotton and the doubling of the chromosome number in the resulting hybrid.

Further evidence that allopolyploidy has played an important role in evolution is derived from the artificial synthesis of polyploids. Beasley (1942) resynthesised an allotetraploid cotton from hybrids of the wild American *Gossypium thurberi* and the old-world *G. arboreum*, both diploid ($2N=26$). The tetraploid with 52 chromosomes was similar to the commercial American tetraploid cotton and crossed successfully with the latter. An undisputed case of the synthetic production of a natural allotetraploid is that of *Galeopsis tetrahit* by Muntzing. This wild species, a member of the mint family, has 32 chromosomes. Muntzing crossed *G. speciosa* and *G. pubescens*, both with 16 chromosomes, and among the offspring of their hybrids appeared some plants with the doubled number of chromosomes (32). These were identical with the wild *G. tetrahit* and crossed freely with the latter, producing fertile hybrids. In short, Muntzing had resynthesised in the laboratory *G. tetrahit* which must have arisen in nature by a similar process of species hybridisation followed by chromosome doubling in the hybrid. He had only copied the method which had occurred in nature spontaneously. Many other naturally occurring polyploids have been synthesised by species hybridisation and the doubling of the chromosome number by colchicine treatment. With the help of colchicine it is possible to produce artificial allotetraploids between any two species which will cross with each other successfully and produce viable hybrids. It has been estimated that more than half of the higher plants are allopolyploids of one degree or another.

Allopolyploids may be produced not only between species of the same genus but sometimes intergeneric polyploids may also be produced. A classical case of intergeneric allopolyploid is that of the hybrid between radish (*Raphanus sativus*) and cabbage (*Brassica oleracea*) obtained by Karpechenko (1926). The two plants belong to different genera, but they have the same chromosome numbers ($2N=18$). The radish×cabbage hybrid (F_1) had 18 chromosomes, 9 from radish and 9 from cabbage. But there is little homology between the two types of chromosomes, so that they do not pair at meiosis and thus fail to produce normal sex cells. As a result, the hybrid is sterile. But some of the reproductive cells fail to divide at the time of meiosis and produce sex cells with 18 chromosomes. Fertilization between such germ cells produces F_2 plants with 36

chromosomes, 18 of the cabbage type and 18 of the radish type. These plants, which were tetraploids, were an entirely new species which has been called *Raphanobrassica*. The plants, in which the root is like cabbage and foliage like radish, are tall and vigorous. These allotetraploids have 18 radish and 18 cabbage chromosomes and there is no difficulty in pairing at meiosis. The 18 radish chromosomes form 9 pairs and the 18 cabbage chromosomes form 9 other pairs. Meiosis is normal and sex cells have 18 chromosomes, 9 radish and 9 cabbage. *Raphanobrassica* is, therefore, fully fertile. Moreover, it breeds true and is reproductively isolated from its own ancestors, the radish and cabbage, with which it crosses with difficulty forming triploid ($3N=27$) hybrids which are mostly sterile.

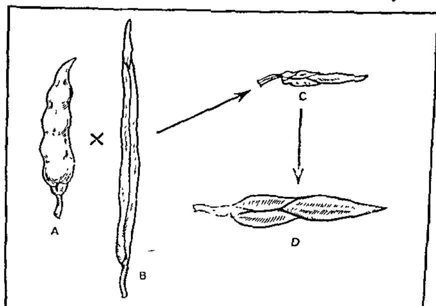


Fig. 17 1. Origin of *Raphanobrassica* by allopolyploidy. A, fruit of radish (*Raphanus*); B, cabbage (*Brassica*), C, sterile diploid hybrid (9R+9B) between radish and cabbage; D, tetraploid *Raphanobrassica* (18R+18B) produced by chromosome doubling of C

The allotetraploid *Raphanobrassica* is thus a new species by any definition. It has been produced by copying a method which has been used in nature on a large scale at least in the plant kingdom over a length of time which is counted in terms of geological periods. The production of this new species is a direct proof of evolution and indicates one of the mechanisms by which new forms of life have arisen from older ones in nature. While in the case of mutations it could be said that the mutated cotton is still cotton and mutated horse a horse, no such argument can be brought

forward in the case of *Raphanobrassica*. The doctrine of evolution thus stands established. Allopolyploidy has played an important, though not exclusive, role in the evolution of plant kingdom.

Polyploids have a larger number of genes and chromosomes There is thus a greater material for gene and chromosomal mutations than in diploids resulting in greater evolutionary variability. A gene mutation has less chance of showing its effect in a polyploid than in a diploid form because for every mutated gene the polyploid has a larger number of normal genes. The deleterious effect of any mutation will, therefore, be masked by the normal genes. A favourable mutation will, however, increase the chances of selection and survival. Polyploidy has been responsible for the evolution of the perennial habit from the annual habit. It has been an important method by which duplicate and multiple factors have been produced in evolution.

In the natural production of polyploids, interspecific hybridisation has been more frequent than between species belonging to different genera. In plant genera, where several species possess chromosome numbers which form a series of multiples of some low basic number, the probability is great that these species have been formed by the method described above. This has been the case with wheats and related grasses which have 14, 28 and 4? chromosomes, the basic number being 7. We have already seen above that the American cultivated species of cotton owe their origin to allopolyploidy. Among other polyploid species are oats, maize, sugar-cane, alfalfa, tobacco, potato, sweet potatoes, banana, plum, certain varieties of apples and pears, strawberries, dahlias, roses, irises, lilies, tulips, and hyacinths.

SPECIATION AND NATURAL SELECTION

In the preceding pages have been described the various mechanisms by which heritable variations arise in nature. The process of hybridisation between individuals belonging to different species of the same genus or even different genera followed by polyploidy leads to the development of new species in one step. Allopolyploidy has played an important role in evolution in the plant kingdom. It represents a short-cut in evolution by which a genus may adapt itself more rapidly than by mutation and recombination to a rapidly changing environment.

The variations produced by mutations and chromosomal rearrangements are of small magnitude, and the development of new species through them is a very slow and long process. These small

variations pile up in several generations until they result in the formation of races within a species. A further step in evolution is the isolation of these races so that they are prevented from crossing between themselves and with the parental forms. The isolation may be geographical, ecological or reproductive. In the last category are included such isolating mechanisms as different seasons of flowering, structural peculiarities of the flower which hinder cross-pollination, infertile and inviable hybirds, failure of the pollen grain to germinate or for the pollen tube to grow, etc. These isolated groups are then subjected to the action of natural selection which gradually eliminates the unfavourable genes and gene combinations. As a result of further variations arising in them, these groups diverge more and more from one another. Ultimately, as a result of divergent adaptations to their environments these races become fairly differentiated to be regarded as sub-species within the ancestral species. The whole process is very slow and may take thousands of years. New mutations in these sub-species bring about further changes in gene combinations and finally the sub-species become established as new species.

The slow mechanism of evolution by isolation has played a more important role in nature than that of polyploidy. In either case, natural selection plays a directive role. If the new species is adapted to the environment, it will flourish, otherwise, it will be worsted in the struggle for existence.

Natural selection, however, does not appear to be an all-or-none phenomenon as was once supposed. According to this, either an organism had favourable variations and survived or it died in the struggle of existence without leaving offspring. Selection does not appear to operate in such a severe fashion. Rather, individuals having only a slight advantage will have a somewhat lower death rate than their unfortunate cousins and will leave somewhat more numerous descendants. Conversely, those that have slightly unfavourable variations will have a somewhat higher death rate and will leave somewhat fewer progeny. The net result will be a gradual increase of the favourable variations in a species and a gradual decrease of the unfavourable ones, ultimately resulting in the disappearance of the latter in course of evolution. This differential perpetuation of the genes is selection Natural selection, thus, must be regarded as a mild force rather than a severe one. The changes that it effects are gradual rather than all-or-none.

QUESTION

1. Explain the modern concept of the mechanism of evolution.

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ORIGIN OF LIFE

GOING back from the present to the remote past in the history of our earth we find that things have not always been the same. Nature around us today is the product of a gradual process of evolution that has been going on imperceptibly but slowly and surely over a period of crores of years in the history of this earth. The earliest living forms which inhabited this earth were of a very simple type and slowly and progressively they became more and more complex and this process continued till the present-day plants and animals, specialised in many ways, came into being.

We have learnt that protoplasm and life never arise *de novo*. Life arises only from pre-existing life. All the present-day living forms must then be the direct descendants of the first living thing which appeared on this earth in its early history. The origin of life is indeed a very interesting question. It is not possible now to generate life from inanimate objects. The origin of first life must then have taken place under conditions which no longer exist now.

Some people suppose that life on this earth must have come from some other planet. This only shifts the place of origin of first life to some other heavenly body. There is no proof of the existence of life on other planetary bodies. Moreover, it is doubtful if such life could survive the journey from one planet to the other.

An essential feature of living things, apart from such properties as growth, irritability and reproduction, is that the living matter is composed of complex organic compounds. Of these the basic compounds are carbohydrates, lipids (fats and fat-like substances) and proteins. Of these the first two are store-houses of energy. Most of the properties of protoplasm are due to its protein component. The protoplasmic proteins are in the form of nucleoproteins which are formed by a combination of proteins and nucleic acids. The proteins

are formed from amino-acids by a process of condensation in which hundreds of molecules of amino-acids are lined together, giving rise to molecules of large size. The proteins and nucleic acids are synthesised only in the bodies of living organisms and cannot be produced from inorganic substances outside the living beings. The origin of life is, therefore, linked with the primary formation of compounds like proteins from inorganic substances.

Evidence in support of the hypothesis that the nucleoproteins are the basic material of life is provided by the study of **filterable viruses**. These are the simplest of living organisms. These are much smaller than the tiniest of bacteria and are so small that they are not visible under the ordinary microscope. They pass through filters of unglazed porcelain through which bacteria cannot pass. They can be seen only with the help of electron microscope and appear as rod-like or crystalline bodies.

An important feature of the viruses is that they are obligate parasites which develop only in the living cells of plants or animals. They are not known to occur outside the bodies of their hosts Some of them are responsible for dangerous diseases like small pox, poliomyelitis, yellow fever, measles, influenza and common cold. Plant viruses cause serious damage to crop plants and consequent loss. In spite of their small size, the viruses are complex structures and are regarded as degenerate pieces of protoplasm derived from larger organisms such as bacteria. A well-known plant virus is tobacco mosaic virus. It is crystalline in appearance and is one of the simplest viruses. Chemically, it has been found to be a nucleoprotein with a molecular weight of 5 crores

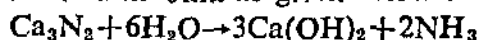
A characteristic feature of the viruses, which puts them in the category of living organisms, is their ability to multiply and reproduce in the living cells of their hosts. When a small amount of the virus protein which causes the mosaic disease in tobacco is injected into the healthy plant, the disease develops in a few days and the amount of virus proteins in the infected plant increases rapidly to about a million times the amount injected in the healthy plant. Although the tobacco virus does not possess the organized structure characteristic of living organisms, it must be regarded as living thing or at least lying on the borderline between the living and the non-living. This conclusion is arrived at as a deduction from the fact that the virus reproduces itself at the expense of the materials obtained from the tobacco leaves. The fact that the virus has a nucleoprotein nature supports this conclusion.

Another conclusion that we draw from the study of the tobacco mosaic virus is that the nucleoproteins are the basic material of life. The origin of life then boils down to the origin of nucleoproteins. The Russian scientist Oparin and several other scientists have put forward a plausible hypothesis as to how chemically substances which now can be formed only in living organisms, might have been formed without the intervention of life under the conditions which prevailed in the early days of the earth's history.

According to geologists, our earth is about 450 crore(4·5 billion) years old. It is a small part of our sun which was spilt off from the parent as a result of a tidal wave which was raised when another star approached our sun. At that time the earth was a hot gaseous mass with a surface temperature of 6000° to 8000°C. As this hot mass cooled, the heavy metals, especially iron, moved to the centre carrying carbon with it. With further cooling the carbon combined with the metals forming carbides like CaC_2. Carbides are the most stable carbon compounds at high temperatures. This process was slow and took crores of years.

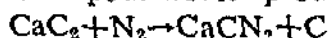
The earth's original atmosphere did not contain any free oxygen or nitrogen. Water vapour occurred in the form of superheated steam. The carbides reacted with water vapours to produce some simple hydrocarbons such as methane.

Nitrogen occurred in the form of stable nitrides of metals like iron, calcium, aluminium or magnesium. These reacting with water vapour would produce ammonia as given below :—



$$Ca_3N_2+6H_2O \rightarrow 3Ca(OH)_2+2NH_3$$

or nitrogen would first react with carbides forming cyanamides and these reacting with water vapour would produce ammonia ;



$$CaC_2+N_2 \rightarrow CaCN_2+C$$



$$CaCN_2+3H_2O \rightarrow CaCO_3+2NH_3$$

With the cooling of the earth the water vapour condensed into liquid water. The water molecules, split into *H* and (*OH*) ions combined with hydrocarbons producing alcohols, simple aldehydes like formaldehyde, ketones and organic acids. These reactions were made possible because high energy ultraviolet rays were then reaching the earth's surface. These are now absorbed in the upper atmosphere by oxygen and ozone. Ammonia reacting with organic acids would give rise among other compounds, to amino-acids. The liquid water would then be forming hot oceans on the earth. This hot water must have contained many of these and other compounds in solution. Once the amino-acids were formed the formation of

polypeptides and proteins through the process of condensation and polymerization must have taken place in much the same way as it occurs now. None of these nitrogenous organic compounds were alive, but life was on its way. Nature had taken the first step towards the evolution of Life.

Besides proteins many other complex organic compounds must have been produced in the hot waters of the oceans in those early days. Among these were fats and substances like cellulose and keratin. Many of them must have been substances with large molecules. These formed colloidal particles with water absorbed on their surfaces. Some of these colloidal particles must have been capable of adsorbing other substances from the environment and must have been able to assimilate these substances and to grow in size at their expense. If we consider growth as the criterion of life then here is something which is near being alive. A continuation of this process must have led to the production of particles which could duplicate themselves at the expense of the material obtained from the environment. This would have been the first step towards self-reproduction, an important characteristic of the living organisms. This was a major step in the evolution of life. The first living particle may have been something like a simple virus which, unlike the present-day viruses, must have been able to multiply at the expense of the inorganic or organic non-living substances present in the environment.

The above account is an outline of what would have been possible or even probable-under the conditions in the early history of the earth according to the conception of Oparin and many others and is widely accepted.

The question may well be asked, could life originate now? The origin of life is preceded by the production of organic substances. The question would thus be whether under the present conditions organic substances could be produced and accumulated in the inorganic environment. The answer is in the negative. The simple reason for this is that the organic substances would be at once used up as food by the living organisms and would not accumulate in the inorganic environment. The present-day conditions are very different from what they were at the dawn of life. Even if proteins and other organic matter arose in the manner outlined above, outside the living world, they would have almost no chance of accumulating. All such substances would be in water inhabited by many species of animals.

up by these animals as food. Any excess of such organic matter will only help the animals to flourish and soon there would be no excess. Such organic material, if formed, would not be able to escape this fate for long. It is almost impossible for life to originate *de novo* when so much life is already there. Life could originate only when there was no life. Proteins are the major component of protoplasm and most of the properties of protoplasm are due to its protein component. Proteins determine the form and behaviour of organisms and make one organism constantly different from another. The reason for this is that the hundreds of enzymes which are essential for biological matabolism are proteins. Proteins are also responsible for numerous other properties of living things. It is, therefore, no exaggeration when we say that it is the proteins that characterise living things.

QUESTION

1. Write an essay on the origin o f life.